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MICROTUS AND *PITYMYS* (ARVICOLIDAE) FROM CUMBERLAND CAVE, MARYLAND, WITH A COMPARISON OF SOME NEW AND OLD WORLD SPECIES

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Abstract

Microtus guildayi, new species, *M. paroperarius* Hibbard 1944, and *Pitymys cumberlandensis*, new species, are identified in the Irvingtonian Cumberland Cave fauna on the basis of a typological and biometrical analysis of m1 and M3. *P. cumberlandensis* is the earliest known representative of *Pitymys*. Its bearing on the relationship of *Pitymys* and *Microtus* is discussed. Comparison of the Cumberland Cave *Microtus* species with other North American and European relatives leads to 1) the Middle Irvingtonian age determination of the Cumberland Cave deposits, 2) the recognition of a North American *Pedomys* lineage, and 3) the assumption of two different *Microtus* migrations from Eurasia to North America during the Middle Irvingtonian (=Early Biharian). The dental evolution in *Microtus* (*Pedomys*) and in the early *Microtus* lineages of Europe is compared. The classifications and the phylogenetic reconstructions of Biharian *Microtus* species suggested by Chaline (1972) and Van der Meulen (1973) are discussed.

Introduction

The Pleistocene Cumberland Cave locality near Cumberland, Maryland, has been known since 1913, when Dr. J. W. Gidley published his preliminary report. A monograph on the fauna, including a compilation of previous studies, was finished by Dr. C. Lewis Gazin after the death of Dr. Gidley (Gidley and Gazin, 1938). Recently Guilday (1971) discussed the Cumberland Cave fauna in his survey of the Pleistocene history of the Appalachian mammal fauna. In this discussion a number

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of additions to Gidley and Gazin's faunal list were given as a result of collecting by Carnegie Museum field parties during the 1960's, which greatly enlarged the collections of smaller mammals.

Included in this new material were the *Microtus* molars, which Guilday discussed in an unpublished contribution to the Hibbard Symposium at Ann Arbor in 1974. Gidley and Gazin (1938) recognized a single *Microtus* species, *M.* (or *Pitymys?*) cf. *involutus* Cope. Guilday noted the presence of at least two distinct m1 morphotypes, a three- and a four-triangled one. He emphasized the difficulties in separating and determining the *Microtus* species on m1's (first lower molars) but remarked: "the 4-triangle m1, whatever its taxonomic affinities, serves as a reliable index fossil in Appalachian cave faunas."

His interest being raised but lacking the time to continue the research himself, Guilday kindly invited the present author to study *Microtus* and *Pitymys* in the Carnegie Museum collections from Cumberland Cave.

The large quantity and the comparable morphology of the Cumberland m1's permitted the application of the biometrical analysis that was introduced in a study of Middle Pleistocene *Microtus* m1's from Europe (Van der Meulen, 1973). Material of the earliest North American *Microtus* representative (unnamed) and of the later *Microtus llanensis* Hibbard, *M. paroperarius* Hibbard, and *M. meadensis* Hibbard from midwestern localities has also been measured. Thus, objective comparisons between the examined North American and European species are possible.

Furthermore, the author was given ample opportunity to study dentitions of the living North American representatives of *Microtus* and *Pitymys* [throughout this paper a distinction is made between *Pitymys* and "*Pitymys*." *Pitymys* stands for the author's restricted use of the taxon, "*Pitymys*" for the common use in the literature (see section on the systematics of *P. cumberlandensis*).], not only those of the Carnegie Museum but also of other museums.

In the following sections the biometrical methods will be applied to separate the Cumberland Cave species. After the descriptions of each of these three species follow taxonomic remarks and comparisons with related forms from North America and Europe. Then the biostratigraphical implications for the American localities from which the compared *Microtus* species come, and intercontinental correlations are discussed.

The Middle Pleistocene evolution of *Microtus* in Europe, as interpreted by the author, will be compared to that in North America. Finally, Chaline's (1972) interpretation of early *Microtus* evolution is discussed in order to clarify the confusing differences between Dr. Chaline's and the author's concepts on this matter.

Methods and Materials

Material Studied

Six hundred and eighty-eight *Microtus* and *Pitymys* specimens in the Cumberland Cave collection of Carnegie Museum (CM) have been studied. The collection was made by Allen McCrady and Harold Hamilton and party in 1968. The specimens are numbered partly individually, partly as samples. The include all 208 upper third molars (M3's) of sample CM 20416. The remaining 480 specimens are either isolated m1's (first lower molars) or m1's in lower jaws accompanied or not with m3 and/or m2. Only a minority of the lower jaws and isolated m1's had received a preliminary assignment. Although not all available material (not counted) has been studied, it is safe to assume that a representative collection of m1 and M3 has been seen. Measurements were carried out on the 219 m1's catalogued as CM 20412, which may be regarded as an unbiased sample of the total of *Microtus* and *Pitymys* m1's according to Guilday (personal communica- tion).

The small collection of *Microtus* and *Pitymys* from Cumberland Cave in the United States National Museum of Natural History (USNM), Washington, D.C., consists of the six lower jaws and one m1 published in Gidley and Gazin (1938) as *Microtus* (or *Pitymys?*) cf. *involutus* (Cope).

All *Microtus* material from Conard Fissure, Arkansas, collected by Dr. Russell W. Graham in 1969–1971 and stored in the paleontological collections of the State University of Iowa (SUI), has been studied. The material is part of Dr. Graham's thesis (1972) on the Conard Fissure fauna and has been determined as *M. (Pedomys) llanensis* Hibbard (55 m1's) and *Microtus paroperarius* Hibbard (five m1's). All m1's were measured for this study. Two of Graham's *M. (Pedomys) llanensis* m1's are referred to *M. paroperarius* and two other to *Pitymys cumberlandensis*, new species, for reasons discussed below.

The Museum of Paleontology, the University of Michigan (UMMP), Ann Arbor, loaned material from the localities Wathena, Kentuck and the Sunbrite (Cudahy) Ash Mine in Kansas.

All *Microtus* molars from Wathena in the UMMP collection have been seen. The collection was made by Howard O'Connor, Bob Carr and Claude W. Hibbard in 1969 from two different silt beds below the Nickerson till exposed in a pit south of Wathena, Doniphan Co. The lower silts yielded 17 m1's, the upper silts three m1's. Only the 17
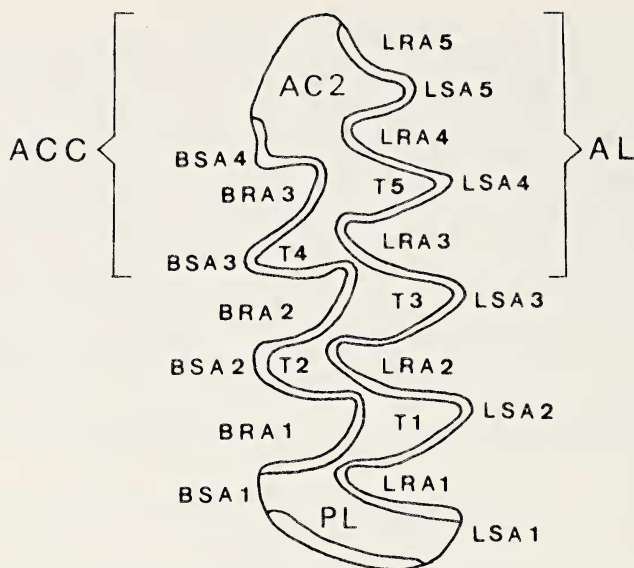
Fig. 1.—Occlusal surface of left m1 of *Microtus* showing the terminology of parts of the occlusal surface after Van der Meulen (1974). AC = anterior cap; ACC = anteroconid complex; AL = anterior loop (European context); B = buccal; L = lingual; PL = posterior lobe; RA = re-entrant angle; SA = salient angle; T = triangle.

m1's from the lower silts are used in the statistical analyses. The fauna from Wathena has been described by Sudi D. Einsohn (1971). She determined the *Microtus* molars as *Microtus llanensis* Hibbard. The greater part of her material is in the University of Kansas Natural History collection, and has not been studied by the author.

Approximately half of the *Microtus* (*Pedomys*) *llanensis* collection from Kentuck (Hibbard, 1952) could be studied. It included 15 measurable m1's.

Seventy seven unidentified *Microtus* m1's and 135 measurable m1's of *M.* ("*Pitymys*") *meadensis* Hibbard have been studied from the Sunbrite Ash Mine, which locality has yielded a great part of the so-called Cudahy local fauna (Hibbard, 1944). Seventy m1's of the unidentified *Microtus* appear to belong to *M. paroperarius*, seven m1's to *M. meadensis*. The Sunbrite Ash Mine is the type locality of both species. The material of the third Cudahy *Microtus* species, *M.* (*Pedomys*) *llanensis*, was on loan and could not be studied.

Dr. Robert A. Martin donated to Carnegie Museum a small collection of *M.* (*Allophaiomys*) cf. *A. pliocaenicus* Kormos from the Java local fauna, South Dakota (Martin, 1973, 1975). Although seen by the author, the Java material is not used in the statistical analyses, because it is presently under study by Dr. Martin.

Dr. R. D. Guthrie kindly sent some material of *Microtus deceitensis* from the Cape Deceit fauna, Alaska (Guthrie and Matthews, 1971).

Terminology of Vole Molars

Upper and lower molars are designated as M and m, respectively. The terminology for the various parts of the molars is after Van der Meulen (1973, 1974). Salient angles

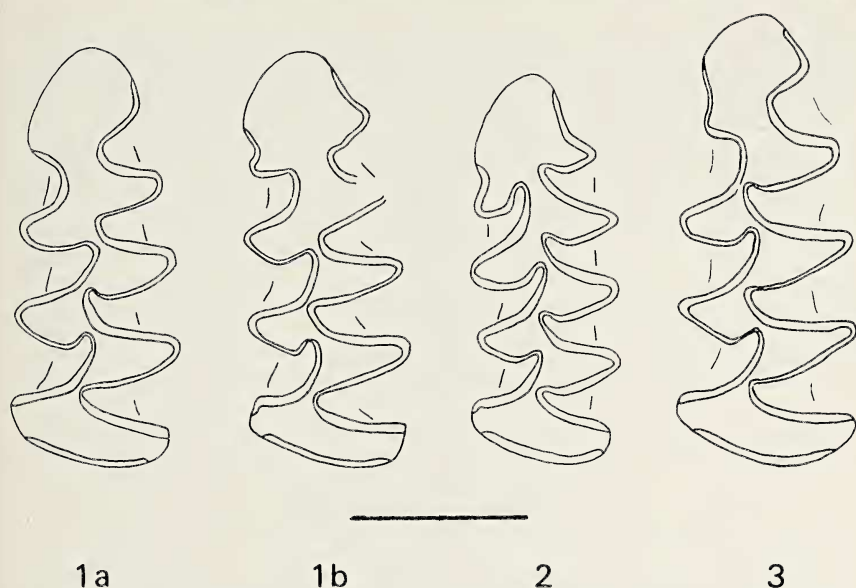**1a**   **1b**   **2**   **3**

Fig. 2.—Occlusal surfaces of four left m1's of *Microtus* and *Pitymys* from Cumberland Cave illustrating the morphotypes. 1a = morphotype 1a; 1b = morphotype 1b; 2 = morphotype 4; 3 = morphotype 2.

(SA), reentrant angles (RA), and triangles (T) are counted from posterior to anterior in lower molars and reversed in upper molars. The first two triangles behind the anterior loop are numbered T1 and T2 in M1, but T2 and T3 in M2 and M3, so that homologous triangles in the upper molar series receive the same number. The terminology of the elements of the occlusal surface of m1 is given in Fig. 1. It is noted that a number of American authors use the term anterior loop for the part of m1, that is called anterior cap in the terminology used here. European authors denote as anterior loop the entire anterior dentine field of which the cap forms the anteriormost part.

Observations and Parameters for Quantitative Analysis

The microtine species of Cumberland Cave are distinguished by the m1, the relatively rare lower jaws provide some information on the morphology of associated m2's and m3's. These m2's and m3's will be described under the species description. M1 and M2 have not been studied. The patterns are all normal for *Microtus*. *Pitymys* M1 and M2 might have been separated on thickness of enamel.

The object of study is the enamel pattern of the occlusal surface of m1 and M3. The first lower molar is the best single available tool for distinguishing fossil vole species. This is confirmed by observations from living species, in which clearly different m1 patterns characterize different species. On the other hand, closely related species, of *Microtus* in particular, do not always differ in m1 patterns. This implies that paleontologists may not recognize all fossil vole species, an unknown number of the taxa containing possibly more than one species.

Time and again the great variability of the diagnostic anteroconid complex of m1 has been emphasized in the literature. This difficulty can, however, be met by adopting high
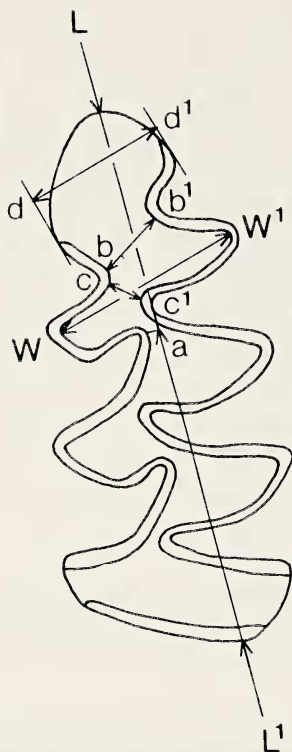
Fig. 3.—Occlusal surface of a left *Microtus* m1 illustrating the measurements. L-L' = L; a-L = a; W-W' = W; d-d' = w'; b-b' = b; c-c' = c. The ratio A/L = 100 a/L is a measure for the relative length of anteroconid complex; the ratio W'/W = 100 w'/W for the relative width of the anterior cap; the ratio B/W = 100 b/W for the degree of confluency between anterior cap and triangles 4 and 5; the ratio C/W = 100 c/W for the degree of confluency between triangles 4 and 5.

confidence levels in statistical tests of differences between samples. The great variation certainly discredits a typological approach.

Morphology of m1

Lower first molars from Cumberland Cave are divided into three groups characterized by three different morphotypes (Fig. 2) numbered 1, 2 and 4 to achieve standardization with those in Van der Meulen (1973).

Morphotype 1 has an occlusal surface consisting of a posterior loop, three closed triangles and the anteroconid complex (ACC) consisting of a single dentine field. The lingual salient angles are deeper than the buccal ones; the reentrants are wide, two of them (BRA3 and LRA4) are shallow. In the middle of the posterior part of the reentrants there is usually a definite bend in the enamel. The enamel is clearly thinner on the posterior margin of all salient angles than it is on the anterior margin.

This morphotype is the same as morphotype 1 in Van der Meulen (1973), and, likewise, a distinction can be made between a more simple type 1a (Fig. 2, 1a) with broadly confluent parts of the ACC and with rounded AC2, and a more advanced type 1b (Fig. 2, 1b) in which the AC2 bears incipient salient and/or reentrant angles and one or more of the ACC parts (T4, T5 and AC2) may have narrow connections.

Morphotype 2 is characterized by the ACC being divided in two or, rarely, three fields. As a result there are four or five closed triangles. The AC2 is usually provided with two, more or less pointed, salient (BSA4 and LSA5) and shallow reentrant angles. In all other characters morphotype 2 resembles morphotype 1. This morphotype is the same as morphotype 2 as defined in Van der Meulen, 1973.

Morphotype 4 shows three closed triangles and an ACC consisting of a single field (Fig. 2, 2). It is distinguished from morphotype 1 and 2 by a) having thick enamel, which is thinner only at the tip of the reentrants, b) smaller lingual salient angles as a result of which lingual and buccal salient angles have almost the same width, c) narrow reentrants of which the posterior parts only rarely show a definite bend in the enamel, and d) a deep BRA3 and LRA4 of which the tips point more or less anteriorly.

The connections between the parts of the ACC are often narrow, and AC2 usually bears a well-developed BSA5 and LSA5 and an incipient BRA4 and LRA5. This morphotype is not known from the Middle Pleistocene of Europe.

All *Microtus* m1's from Wathena and Kentuck belong to morphotype 1. Type 1b is rare. In contrast, type 1b is more common relative to type 1a in the morphotype 1 group from Cumberland Cave. The *M. (Pedomys) llanensis* m1's from Conard Fissure virtually all belong to type 1b, a few belonging to type 1a. It seems that the morphotype 1 assemblage from Cumberland Cave is intermediate between the more primitive assemblages from Wathena and Kentuck and the more advanced *M. (Pedomys) llanensis* from Conard Fissure. This morphological series is mainly based on presence and degree of development of salient and reentrant angles at the AC2.

Two specimens from Conard Fissure determined as *M. (Pedomys) llanensis* fit the characterization of morphotype 4. *Microtus paroperarius* from the Sunbrite Ash Mine and Conard Fissure belong to morphotype 2.

The *Microtus meadensis* m1's from the Sunbrite Ash Mine do not fit one of the three morphotypes. In *M. meadensis* T4 and T5 are widely communicating, whereas the anterior loop is separated. First lower molars bearing these features have been distinguished as morphotype 3 in Van der Meulen (1973) and are characteristic of the "*Pitymys*" species of the European Middle Pleistocene.

Measurements of m1

The measurements used here are consistent with those in Van der Meulen (1973) (Fig. 3). Measurement w' is introduced here for the width of the AC2 measured parallel to W. The ratio 100 w'/W = W'/W is a measure of the observed increase of the width of the AC2 due to addition of salient angles in the morphotype 1 series from Wathena and Kentuck, through Cumberland Cave, to Conard Fissure.

The morphotype 4 molars from Cumberland Cave are mainly characterized by thickness of enamel and shape of the salient and reentrant angles. No satisfactorily standardized measurements were found that could quantify these characteristics.

The measurements were made by a Leitz Ortholux microscope with moving stage.

Separation of the Three m1 Morphotypes from Cumberland Cave

In order to examine the reality of the three morphotypes from Cumberland Cave, 219 m1's (CM 20412) were measured. Morphological separation resulted in the determination of 96 m1's of morphotype 1, 71 m1's of morphotype 2 and 52 m1's of morphotype 4.

Fig. 4 shows the distribution of C/W values (the degree of confluency between the
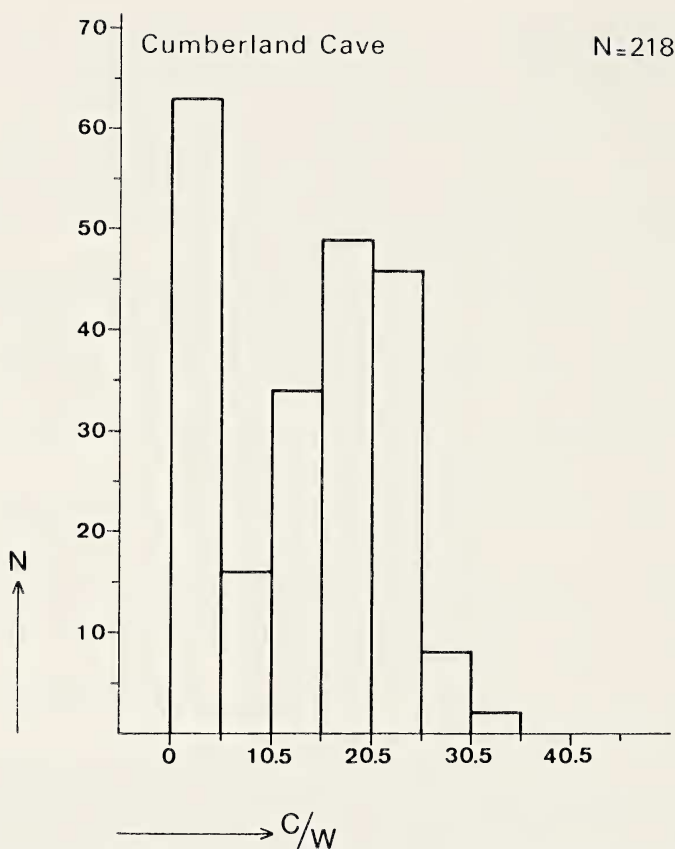
Fig. 4.—Histogram of C/W for all *Microtus* and *Pitymys* m1's from sample CM 20412, Cumberland Cave. The bimodal distribution suggests the presence of two groups.

triangles 4 and 5) of all m1's of the sample. The distribution is bimodal because of the high frequency (N = 63) in class C/W = 0–5, which is separated by class C/W = 6–10 with low frequency (N = 16) from the classes C/W = 11–15 through C/W = 21–25, again with high frequencies. The biomodality is accepted as proof that morphotype 2, that is the four-triangled form, can be biometrically isolated from the two three-triangled morphotypes. Some overlap does exist—nine m1's in class C/W = 6–10 and one m1 in class C/W = 11–15 are assigned to morphotype 2 on secondary features such as the type of enamel thickness and shape of the ACC.

As noted in the previous section no measurements were found to quantify the primary differences of morphotypes 1 and 4, but the features of morphotype 4 are clear enough to leave virtually no undetermined m1, and taxonomically important enough to permit this typological separation.

Fig. 5 shows that morphotype 1 and 4 differ clearly in their relationship between b′ and w′. Morphotype 4 combines lower b values with higher w′ values in comparison to
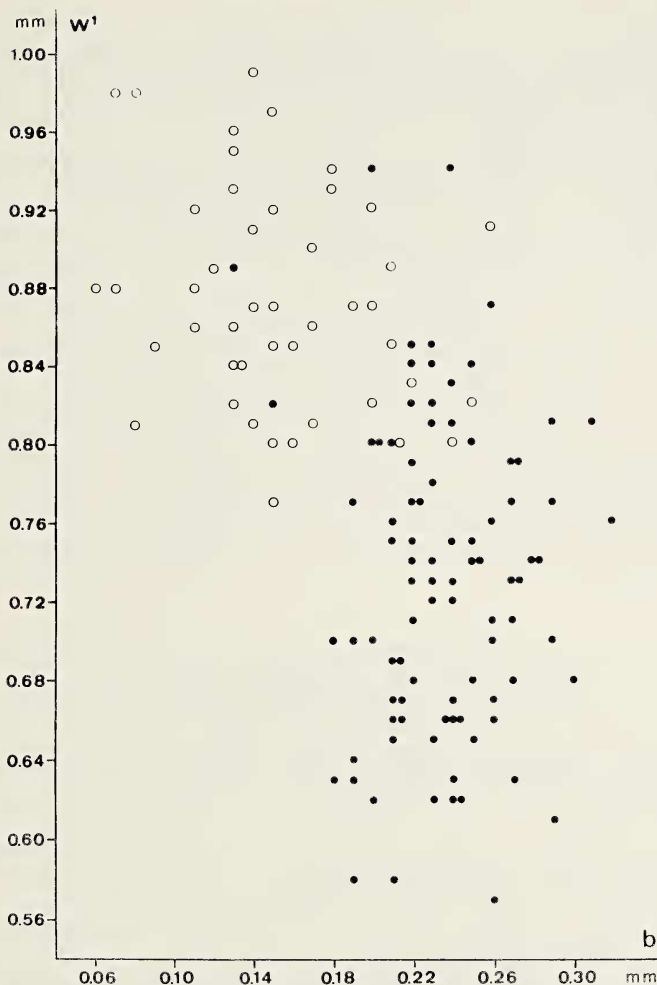
Fig. 5.—Relationship between b and w' for the morphotype 1 (*Microtus guildayi*, new species, solid circles) and morphotype 4 (*Pitymys cumberlandensis*, new species, open circles) m1's from sample CM 20412 from Cumberland Cave.

morphotype 1. This relationship is independant of the criteria used to distinguish the two morphotypes. The observed differences in this relationship, therefore, support the typological differentiation.

Other measurements will be discussed as appropriate in the systematic discussion of the Cumberland species—*Microtus* (*Pedomys*) *guildayi*, new species (equals the morphotype 1 m1's), *M. paroperarius* Hibbard (equals the morphotype 2 m1's) and *Pitymys cumberlandensis*, new species (equals the morphotype 4 m1's).

Morphology of M3

A study of 208 M3's in sample CM 20416 resulted in the distinction of three different groups characterized by three morphotypes A, B and C (Fig. 6), which are based on the number of reentrant angles that contain crown cementum and the degree of differentiation of the enamel thickness.

Morphotype A is characterized by having 1) well-differentiated enamel thickness, 2) two buccal and two lingual reentrant angles filled with crown cementum, and 3) alternating triangles T2 and T3, that is, the two anteriormost triangles.

Morphotype B is characterized by having 1) very little differentiation of the enamel thickness, 2) two buccal and two lingual reentrants filled with crown cementum, and 3) almost opposed triangles T2 and T3.

Morphotype C is characterized by having two or three buccal and three lingual reentrants filled with crown cememtum. In other respects, it resembles type A.

Two molars are intermediate between types A and B, and have not been determined. Ninety-seven M3's are assigned to type A, 21 to type B, and 88 to type C.

It is very likely that morphotype B M3's should be associated with the morphotype 4 m1's, because they have the thick, little differentiated enamel in common. The more simple M3's of type A are associated with the three-triangled m1's (type 1), the more complexed M3's (type C) with the four-triangled m1's by analogy with living species such as *Microtus* (*Pedomys*) *ochrogaster* and *Microtus oeconomus* with three and four-triangled m1's respectively.

The M3's have not been measured. They will be described in more detail under the species descriptions.

SYSTEMATIC ACCOUNTS

Microtus (Pedomys) guildayi, new species
Fig. 7A–I, Q–R

Holotype.—Damaged right mandible with m1–m2, Fig. 7A; CM 20333.

Figured paratypes.—Fig. 7B–I.

Horizon and type locality.—Irvingtonian Cave filling of Cumberland Cave, near Cumberland, Maryland.

Derivatio nominis.—In honor of John E. Guilday of the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Referred specimens.—At the Carnegie Museum—Fragmentary jaws with one or more molars: CM 20339, CM 20340, CM 20345, CM 20348, CM 20357, CM 20358, CM 20360, CM 20362, CM 20365, CM 20368–20371, CM 20379, CM 20381, CM 20385, CM 20389, CM 20390, CM 24239. Isolated m1's: CM 20397, CM 20398, CM 20401, CM 20404, CM 20405, CM 20407, CM 20408, CM 20416 (27 m1's), unnumbered (41 m1's). Isolated M3's: CM 20416 (79 M3's). At the U.S.N.M.—USNM 7772 (jaw), 12368, 12369, 12370. All specimens are from Cumberland Cave.

Diagnosis.—Medium sized *Microtus* species, with lengthened and somewhat complicated anteroconid complex; the mean of A/L equals or is greater than 44.5, but is less than 46.3; the mean of B/W equals or is greater than 23.0 but is less than 28.0; the mean of C/W equals or is greater than 20.0; the mean of W'/W equals or is greater than 76.0 but is less than 85.0.
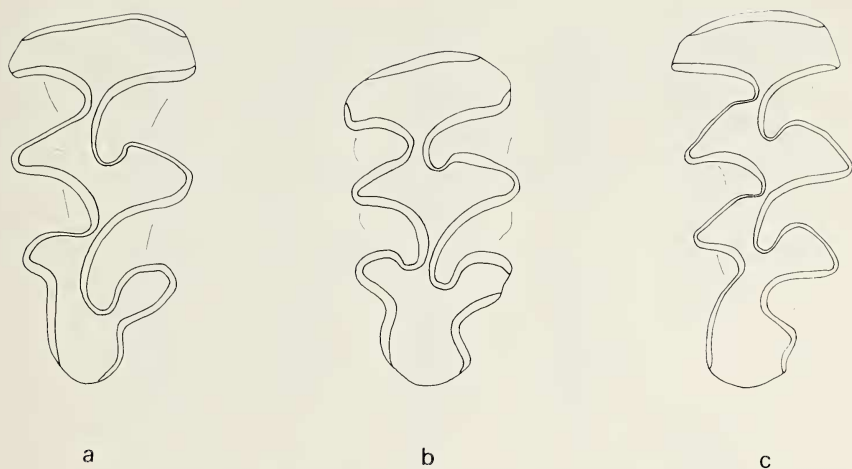
a b c

Fig. 6.—Occlusal surfaces of three right M3's of *Microtus* and *Pitymys* from sample CM 20416, Cumberland Cave, illustrating the three morphotypes—a = morphotype A; b = morphotype B; c = morphotype C.

Differential diagnosis.—*Microtus guildayi* differs from *Microtus* sp. from Wathena and Kentuck in having higher mean A/L and W'/W values and lower mean B/W and C/W values; *Microtus guildayi* differs from *Microtus llanensis* Hibbard in having lower mean A/L and W'/W values and a higher mean B/W value; it differs from *Microtus nutiensis* Chaline and *Microtus burgondiae* Chaline in having a higher mean B/W value.

Measurements.—See Tables 1, 2; Figs. 5, 8–10. Holotype: length m1–m2 = 4.53; a = 1.32, L = 2.84, W = 0.97, w' = 0.81, b = 0.20, c = 0.16, A/L = 46, W'/W = 84, B/W = 21, C/W = 16.

Description

m1.—The morphological description is based on about 200 specimens. All belong to morphotype 1 described in a previous section. The variation of the molars concerns the depth of LRA3, LRA4, and BRA3, and the shape of the anterior cap (AC2). The latter may be rounded (in some 20%), but the majority is provided with one or more incipient features (LSA5, LRA5, BSA4, BRA4). The additional reentrant angles LRA5 and BRA4 are always shallow, usually narrow, and never contain crown cementum. LSA5 and BRA4 are always shallow, usually narrow, and never contain crown cementum. LSA5 and BSA4 are well developed in 11% of the m1's (Fig. 7I). The most common variants are those resembling the holotype and having an incipient BSA4 (accompanied or not with a very narrow BRA4) and a more or less rounded lingual part of the AC2.

m2.—Nineteen m1 bearing jaws of *M. guildayi* are associated with a m2. T3 and T4 are connected in all these m2's. T1 and T2 are separated in 11 m2's and slightly communicating in the remaining eight specimens.
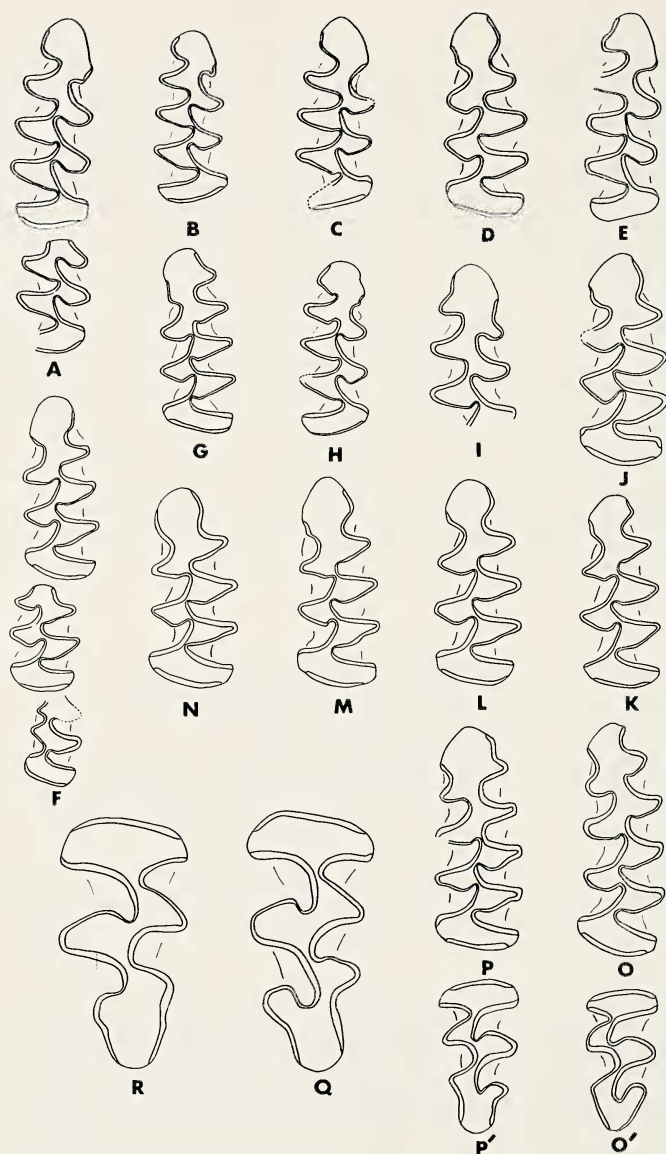
Fig. 7.—*Microtus* (*Pedomys*) *guildayi*, new species, from Cumberland Cave, Maryland—A) right m1-m2, CM 20333, holotype; B, C, E, H, I) right m1 from sample CM 20412 (PL and T1 missing in I); D, G) left m1 from sample CM 20412; F) left M1-M3, CM 20379; Q, R) left M3 from CM 20416. *Microtus* (*Allophaiomys*) sp. from sample Wathena, Kansas—J–L) left m1 from sample UMMP V50609. *Microtus* (*Allophaiomys*) sp. from sample Kentuck, Kansas—M, N) left m1 from UMMP V50516. *Microtus* (*Pedomys*) *ochrogaster* from Greenwood Co., Kansas—O, O') left m1 and right M3, CM 21529; P, P') left m1 and right M3, CM 20793.
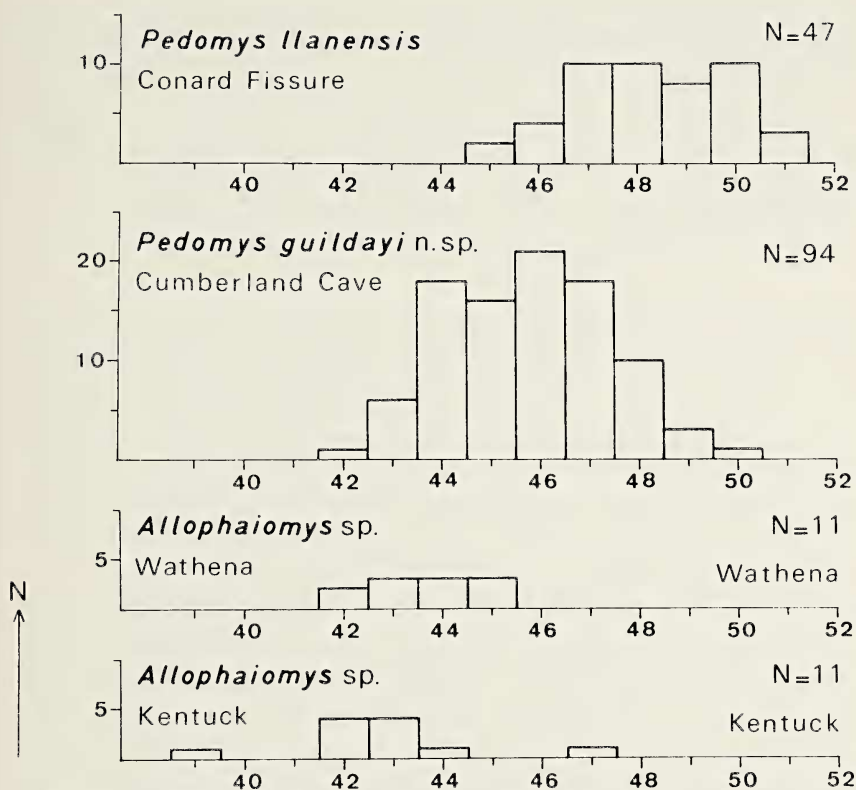
Fig. 8.—Histograms of A/L for the m1 samples of the studied *Microtus* (*Allophaiomys*) and *M.* (*Pedomys*) species.

m3.—The three m3's that could be identified as *M. guildayi* have three dentine fields. Their BSA3 is small.

M3.—The 97 M3's of CM 20416 belonging to morphotype A (see above) are determined to be *M. guildayi*. The two triangles (T2 and T3) behind the anterior loop are separated in eight specimens; in the remainder they are communicating to a greater or lesser degree (Fig. 7Q–R). Very rarely is T3 confluent with T4. The latter almost always opens into the short posterior loop. T4 and LSA3 are variably developed and may be incipient (Fig. 7R). The shallow folds at the posterior loop may be absent.

Systematic Position

Microtus guildayi fits the definition of the subgenus *Allophaiomys* Kormos, which is considered to include the fossil *Microtus* species in which the majority of m1 belong to morphotype 1 (three triangled), that is, the mean of B/W equals or is greater than eight, the mean of C/W equals or is greater than eight (Van der Meulen, 1973: 96). However,

Table 1.—*Comparison of b and w' from ml's of* Microtus guildayi *new species (morphotype 1), and* Pitymys cumberlandensis, *new species (morphotype 2), from Cumberland Cave (sample CM 20412).*

Species	N	Mean ± SE	SD	Range	Parameter
Microtus guildayi	101	0.236 ± 0.003	0.033	0.13–0.32	b
Pitymys cumberlandensis	50	0.154 ± 0.007	0.047	0.06–0.26	
Microtus guildayi	90	0.730 ± 0.008	0.080	0.57–0.94	w'
Pitymys cumberlandensis	46	0.874 ± 0.008	0.056	0.77–0.99	

three-triangled ml's are also typical of the living subgenera *Phaiomys* Blyth from Asia, *Pedomys* Baird from North America, and *Orthriomys* Merriam from Mexico. The latter monotypic (sub)genus shows a number of dental features, which it shares only with the equally monotypic *Herpetomys* from Guatemala. These features are the thin, little differentiated enamel, and the large and tightly closed triangles including T1 and T2 of m3. It seems to be largely a matter of taste whether *Orthriomys* and *Herpetomys* would be included in *Microtus* at all, or if they should be placed together in a separate genus.

Allophaiomys, Phaiomys, and *Pedomys* cannot be separated on the morphology of the dentition. One can draw an arbitrary boundary between *Allophaiomys* species and *Pedomys ochrogaster* (the only living species) on the basis of the W'/W ratio, but the difference being minor, this will hardly satisfy the paleontologist working with a purely morphological concept of taxa. On the other hand, those attempting a natural grouping of species cannot accept the uniting in a single subgenus of *Phaiomys* and *Pedomys,* which seem to have evolved independantly in Asia and North America. The present author, favoring the latter attitude, regards *Allophaiomys* as the stock group of *Microtus,* and retains the names *Phaiomys* and *Pedomys. Microtus guildayi,* therefore, is assigned to *Pedomys.*

In *Allophaiomys* are included the following: *Microtus deucalion* (Kretzoi); *M. pliocaenicus* (Kormos) = *M. laguroides* (Kormos), type species of *Allophaiomys; M. ruffoi* (Pasa); *M. nutiensis* Chaline = *M. (Allophaiomys)* sp. A in Van der Meulen (1973); *M. burgondiae* Chaline = *M. (Allophaiomys)* sp. B in Van der Meulen (1973) assigned by Chaline (1972) to the subgenus *Suranomys* Chaline, which is considered a superfluous name, since it includes *M. nivalis,* type species of the subgenus *Chionomys* Miller; *Microtus* sp. (=*Allophaiomys* cf. *A. pliocaenicus* in Martin, 1975) from the Sappa Fm., Wathena, Kentuck and Java. The following species are assigned to *Phaiomys: Microtus leucurus* (Blanford) type species of *Phaiomys; M. strauchi* Büchner; *M. carruthersi* Thomas; *M. juldaschi* (Severtzow); *M. irene* Thomas; *M. oniscus* Thomas. To *Pedomys* are assigned the following: *M. och-*
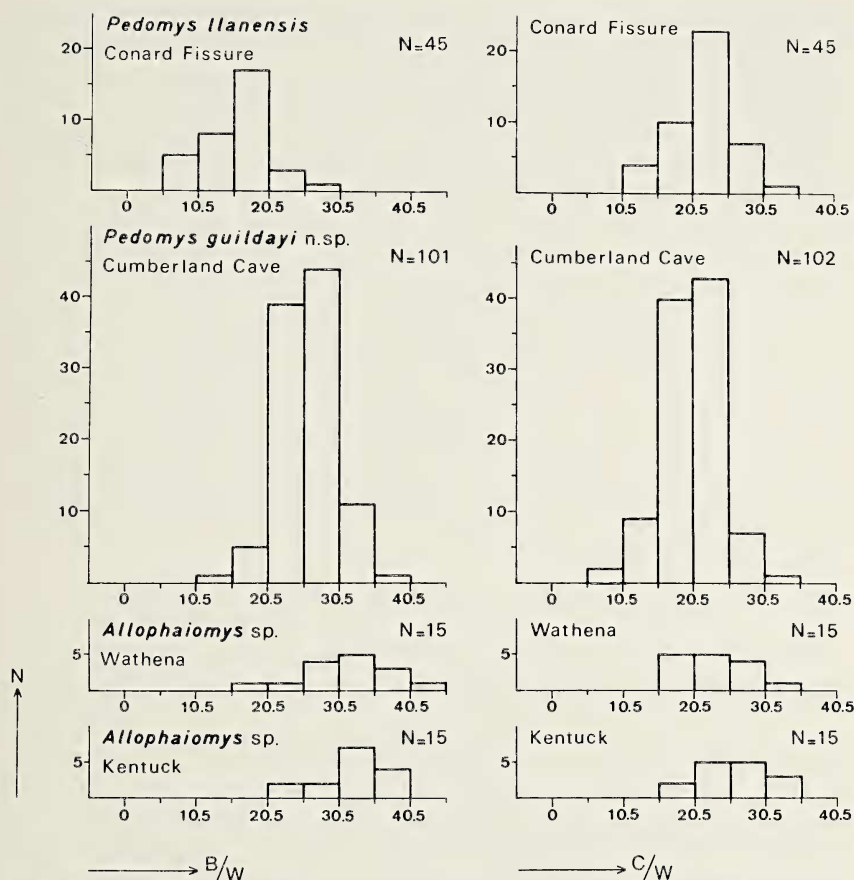
Fig. 9.—Histograms of B/W and C/W of the m1 samples of the studied *Microtus* (*Allophaiomys*) and *M.* (*Pedomys*) species.

rogaster Baird, type species of *Pedomys*; *M. llanensis* Hibbard; *M. guildayi* new species. Only species seen, or adequately figured in the literature (Hinton, 1926; Ognew, 1964) have been considered.

There is a nomenclatorial problem concerning the *Pitymys involutus* Cope 1871, which is better discussed before *Microtus guildayi* is compared to other species. Gidley and Gazin (1938) noted marked similarity in morphology and close correspondence in size between their *Microtus* (or *Pitymys*?) cf. *involutus* (Cope) from Cumberland Cave and the type of *Pitymys involutus* from the Port Kennedy, Pennsylvania locality. Hibbard (1955) reviewed the Port Kennedy arvicolids

and found that the molars of the *P. involutus* holotype were missing. He, therefore, had to follow the description of Gidley and Gazin (1938), who emphasized that Cope's illustrations were incorrect. According to Gidley and Gazin the m1 of the discussed holotype was a three-triangled form resembling the living *P. pinetorum* but having a slightly simpler enamel pattern. Neither Gidley and Gazin, nor Hibbard were aware of the fact that *M.* (?) cf. *involutus* from Cumberland Cave includes three different species (all three being present in the USNM material studied by Gidley and Gazin), two of which have three-triangled m1's—*M. guildayi* and *Pitymys cumberlandensis*, new species. It cannot be established whether the *P. involutus* holotype resembles the *Microtus* species or the *Pitymys* species. Hibbard (1955) found only a single m1 in the existing Port Kennedy arvicolid material, which might belong to *P. involutus* judging from its size. This specimen (Hibbard, 1955: Fig. 2D) seems to belong to *Pitymys*. However, this is not sufficient evidence that the holotype was a *Pitymys* as well. Therefore, and because the Port Kennedy locality has been destroyed (Guilday, personal communication), *Pitymys involutus* Cope 1871 is considered to be a *nomen dubium* and will not be used.

Comparisons with Related North American Species

Microtus guildayi resembles the living *M. orchrogaster* in having a three-triangled m1 and a two-triangled M3. The differences concern the anterior cap of m1, which always bears two well-developed salient angles (LSA5 and BSA4) and shallow reentrant angles (LRA5 and BRA4) in *M. ochrogaster*. These features may be lacking in *M. guildayi* or, if present, are usually smaller. BRA4 in the m1 of the living species normally contains crown cementum, whereas it never does in the Cumberland Cave specimens. In the few *M. ochrogaster* M3's that have been seen, the two central triangles are separated, whereas in *M. guildayi* they are usually communicating.

Microtus llanensis m1's are characterized by the lesser development of the additional features of the AC2 in comparison to *M. ochrogaster*. Since the *M. llanensis* type material was not available, *Microtus guildayi* could only be compared to *M. llanensis* from Conard Fissure studied by Dr. Russell Graham (1972), who directly compared his material to *M. llanensis* from its type locality. He found the two m1 assemblages morphologically identical, and specifically mentioned the "trefoiled anterior loop" (anterior cap in this paper) in the Conard and Cudahy specimens. Some 10% of the *M. guildayi* m1's resemble the central variant of *M. llanensis* in having a trefoiled cap. The differences between the A/L, B/W, and W'/W distributions of *M. guildayi* and *M. llanensis* (see differential diagnosis, Table 2 and Fig. 8) are so great that testing them was considered unnecessary. It further appears that
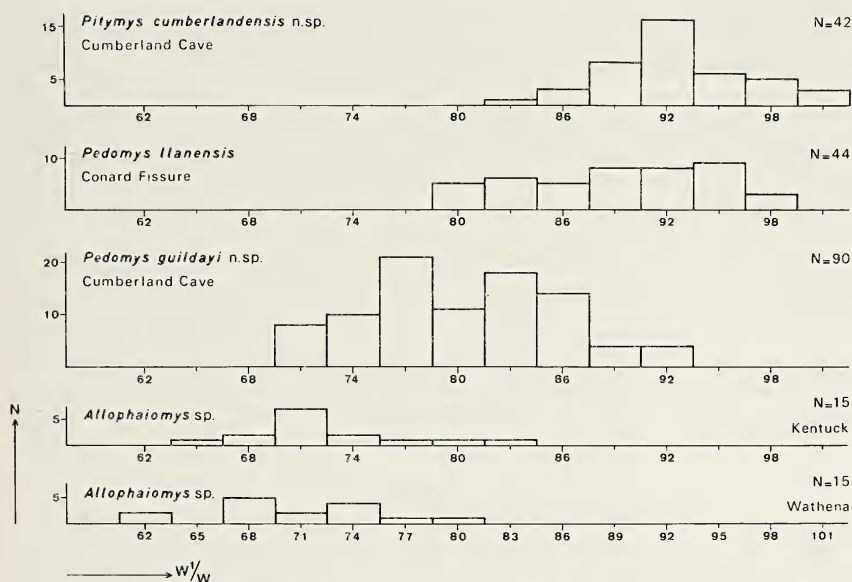
Fig. 10.—Histograms of W'/W for the m1 samples of the studied *Microtus* (*Allophaio-mys*), *M.* (*Pedomys*), and *Pitymys* species.

the *M. llanensis* m1's are somewhat larger than the *M. guildayi* m1's (Table 2).

Microtus molars from Kentuck and Wathena have been determined as *M.* (*Pedomys*) *llanensis* by Hibbard (1952) and Einsohn (1971) respectively. Some 20% of the *M. guildayi* resemble the majority of the m1's from Wathena and Kentuck in the presence of a rounded AC2. Although the number of observations is small, the differences (Table 2, Figs. 8–10) are considered to be large enough to separate the Kentuck and Wathena assemblages from *Microtus llanensis* and *M. guildayi* and to include them in another, probably new, species, which is referred to as *Microtus* (*Allophaiomys*) sp. The naming of this species falls outside the scope of this paper, which deals with part of the Wathena and Kentuck *Microtus* material only.

Allophaiomys cf. *A. pliocaenicus* from the Java local fauna is considered the same species as the one from Kentuck (Martin, 1973, 1975, and my observations). *Microtus* cf. *llanensis* from the type section of the Sappa Formation, Nebraska (Schultz and Martin, 1970; Einsohn, 1971: Pl. 8, Fig. 8), probably belongs to our *Microtus* sp., as well.

Our W'/W and B/W distributions (reflecting the relative width of the anterior cap and the communication between this cap and the fourth and fifth confluent triangles) fully confirm Graham's (1973) observation

Table 2.—*Measurements and ratio data for ml's of* Microtus sp. from Wathena and Kentuck, Microtus guildayi, *new species, from Cumberland Cave and* Microtus llanensis *from Conard Fissure.*

Locality	N	Mean ± SE	SD	Range	Parameter
Wathena	11	2.762 ± 0.033	0.110	2.60–2.92	
Kentuck	11	2.852 ± 0.052	0.173	2.55–3.10	L
Cumberland	94	2.583 ± 0.019	0.181	2.27–3.07	
Conard	47	2.724 ± 0.026	0.176	2.32–3.26	
Wathena	11	43.6 ± 0.34	1.12	42–45	
Kentuck	11	42.7 ± 0.57	1.90	39–47	A/L
Cumberland	94	45.7 ± 0.17	1.65	42–50	
Conard	47	48.3 ± 0.23	1.58	45–51	
Wathena	15	70.7 ± 1.19	4.59	62–79	
Kentuck	15	72.3 ± 4.33	4.33	65–82	W'/W
Cumberland	90	80.4 ± 0.59	5.57	70–91	
Conard	44	89.6 ± 0.86	5.69	80–99	
Wathena	15	31.3 ± 1.53	5.91	20–41	
Kentuck	15	32.1 ± 1.42	5.51	22–40	B/W
Cumberland	101	26.0 ± 0.40	3.97	13–36	
Conard	45	18.8 ± 0.89	5.94	7–32	
Wathena	15	23.1 ± 1.15	4.45	17–31	
Kentuck	15	25.6 ± 1.14	4.40	19–33	C/W
Cumberland	102	20.4 ± 0.40	4.08	9–31	
Conard	45	21.6 ± 0.59	3.93	12–31	

that the anterior cap of "*P. llanensis* from the Kentuck Assemblage (Hibbard, 1952) is a simple crescent-shape as compared to the more trefoiled loop of the Conard and Cudahy specimens. Also the neck between the anterior loop (=anterior cap in our terminology) and the fourth and fifth confluent triangles of the Conard and Cudahy specimens is narrower than that of the Kentuck specimens." Additionally the A/L values (that is, the relative lengths of the anteroconid complex) of the Kentuck and Wathena specimens are considerably lower than those of *M. llanensis*. The Wathena and Kentuck specimens yield nearly identical distributions of the various parameters.

The A/L, W'/W, and B/W distributions of *M. guildayi* are intermediate between those of the Kentuck and Wathena specimens on the one hand and the Conard specimens on the other hand. It is concluded that *Microtus* (*Allophaiomys*) sp. from Wathena and Kentuck, *M.* (*Pedomys*) *guildayi*, *M.* (*Pedomys*) *llanensis*, and *M.* (*Pedomys*) *ochrogaster* belong to an evolutionary lineage, in which the mean of A/L and W/W' increase, while the mean of B/W decreases, reflecting the relative increase of the ACC in comparison to the total length of m1.

This is caused by the addition of new salient and reentrant angles at the anterior cap, while at the same time the communication between the anterior cap and T4 and T5 gets narrower.

This conclusion is almost entirely based on the morphology of m1. There is no independant stratigraphic control on the time sequence of the localities resulting from the assumed *Microtus* evolution, except for the fact that *Microtus* sp. from the Sappa formation comes from a level below the type S Pearlette Ash (Coleridge Ash) dated 1.2 m.y. (=million years) (Zakrzewski, 1975), and that *M. llanensis* from the Cudahy fauna is found directly beneath a type O Pearlette Ash, which has been dated as 0.6 m.y.

The changes found in the "*Pitymys*" lineage in Europe (Van der Meulen, 1975) are fully comparable to those found in the North American lineage described above, which will be referred to as the *Pedomys* lineage.

Comparisons with Related European Species

Microtus (*Allophaiomys*) sp. from Wathena and Kentuck differs from *M.* (*Allophaiomys*) *deucalion* Kretzoi in having greater differentiation in enamel thickness, and probably in the morphology of M3. The four M3's seen from Wathena, the seven M3's from Kentuck, and five M3's from the Java local fauna are of the normal *Microtus* type, whereas in *M. deuclion*, a *Mimomys*-like M3 is common (Van der Meulen, 1974). *Microtus* sp. closely resembles *M.* (*Allophaiomys*) *pliocaenicus* Kormos for which reason Martin (1975) determined the *Microtus* from Java and Kentuck as *Allophaiomys* cf. *A. pliocaenicus*. The ratios A/L and C/W are in accordance with this, but *Microtus* sp. gives mean B/W values, which are intermediate between *M. deucalion* (the mean of B/W = 36.8) and *M. pliocaenicus* (the mean of B/W = 25.3).

The morphology of *Microtus* (*Pedomys*) *guildayi* m1 comes nearest to *M.* (*Allophaiomys*) *nutiensis* Chaline [=*M.* (*Allophaiomys*) sp. A in Van der Meulen, 1975], as far as the shape of the AC2 is concerned. *M. guildayi* differs, however, in having a lower mean A/L and a considerably higher mean B/W value than *M. nutiensis*.

In general, in Europe there are no *Microtus* species with a fairly well-developed AC2 bearing salient and reentrant angles in conjunction with an anteroconid complex composed of a single dentine field, as is characteristic of *M.* (*Pedomys*) species.

These North American species resemble the living, central Asian species, *M.* (*Phaiomys*) *carruthersi* Thomas and, to a lesser degree, *M.* (*Phaiomys*) *juldaschi* Severtsov. In the M3 of *M. carruthersi* T2 and T3 are broadly communicating as in most *Microtus* specimens from Wathena and Kentuck and in *M. guildayi*.

The resemblances are thought to be due to parallel evolution because probable ancestors are known from both continents.
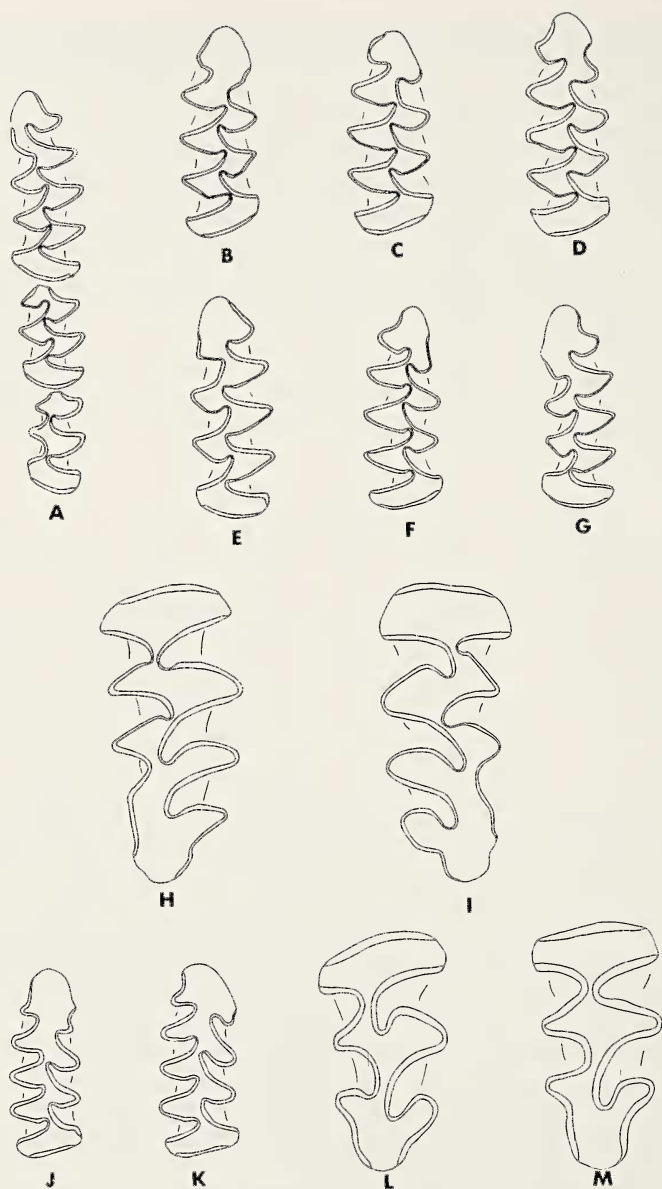
Fig. 11.—*Microtus paroperarius* from Cumberland Cave, Maryland—A) left m1-m3, CM 20347; B–D) right m1 from sample CM 20412; E, G) left m1 from sample CM 20412; F) right m1 from unnumbered sample; H) right M3 from sample CM 20416; I) left M3 from sample CM 20416. *Pitymys cumberlandensis*, new species, from Cumberland Cave, Maryland—J) right m1 from unnumbered sample; K) right m1 from sample CM 20412; L, M) right M3 from sample CM 20416.

Table 3.—*Measurement and ratio data for* Microtus paroperarius *ml's from three localities.*

Locality	N	Mean ± SE	SD	Range	Parameter
Cumberland	60	2.738 ± 0.025	0.192	2.39–3.21	
Sunbrite	46	2.789 ± 0.023	0.154	2.41–3.10	L
Conard	5	2.730 ± 0.076	0.170	2.61–3.01	
Cumberland	60	48.5 ± 0.23	1.76	45–54	
Sunbrite	46	48.2 ± 0.28	1.92	43–52	A/L
Conard	5	48.0 ± 0.71	1.58	46–50	
Cumberland	66	19.2 ± 0.83	6.73	<5–36	
Sunbrite	51	17.5 ± 1.02	7.29	<5–35	B/W
Conard	3	17.3 ± 1.45	2.52	15–20	
Cumberland	74	<5		<5–13	
Sunbrite	54	<5		<5	C/W
Conard	3	<5		<5	

Microtus paroperarius Hibbard 1944
Fig. 11A–I

Locality.—Cumberland Cave, Maryland.

Material.—Mandible with m1–m3: CM 20356; mandibles with m1–m2 or m1: CM 20336–20337, CM 20341–20343, CM 20349–20350, CM 20353, CM 20364, CM 20367, CM 20374, CM 20376–20377, CM 20380, CM 20384, CM 20386, CM 20388; isolated m1's: CM 20396, CM 20399–20400, CM 20402–20403, CM 20406, CM 20412/106, 111, 112, 117, 118, 121–164, 166–195, CM 20416 (37 m1's), unnumbered (42 m1's); M3: CM 20416 (88 specimens). Mandible with m1–m2: USNM 12055.

Measurements.—See Table 3 and Fig. 12.

Description

m1.—Hundred eighty-five m1's of this species have been studied. The counts given below are based on the 152 morphotype 2 m1's in samples CM 20412, 20416, and an unnumbered sample. The variation of this basically four-triangled molar mainly concerns the depth of the reentrant angles shaping the AAC (and hence the number of closed triangles) and the presence or absence and shape of salient angles at the AC2.

The most common variant (±70%) is a four-triangled molar in which BSA4, BRA4, LSA5, and LRA5 are present. The shape of the mentioned reentrant and salient angles is variable. In the remaining 30%, one or more of these features are absent. There are four (2.5%) five-triangled (Fig. 11F) and eight (5%) three-triangled variants (Fig. 11G). In the majority of the BRA4 (90%) and LRA5 (±86%) crown cementum is absent.

m2.—In the nineteen jaws assigned to *M. paroperarius* (including USNM 12055) containing m2, eight m2's have communicating T1–2 and T3–4. In the remaining 11, T1 and T2 are separated and in five of these T3 and T4 are separated as well.

m3.—The single known specimen shows three dentine fields. BSA3 is fairly well developed.

M3 (see also definition of morphotype C).—Behind the AL follow three triangles and the posterior loop, which is provided with a well-developed LSA3 and a LRA3 of LSA4 of variable shape. T2 and T3 are confluent (to a variable degree) in 61 of 88 M3's of CM 20416; in 19 specimens they are almost, and in eight completely, separated.
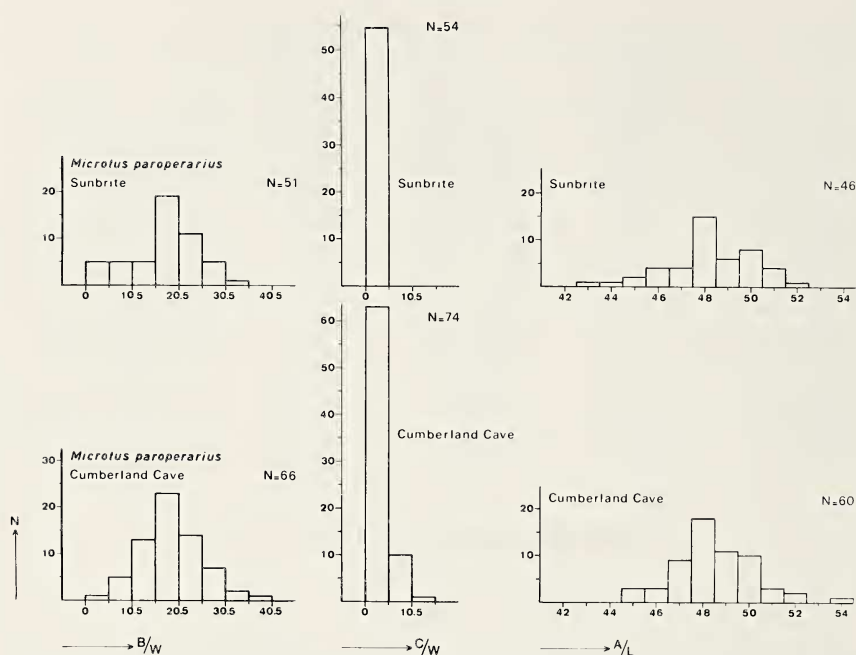
Fig. 12.—Histograms of A/L, B/W and C/W for the m1 samples of *Microtus paroperarius* from Cumberland Cave (CM 20412) and the Sunbrite Ash Mine (UMMP V40299).

Remarks

The Cumberland Cave material has been compared to topotype material of *Microtus paroperarius* from the Cudahy Ash Mine (Sunbrite). There is great resemblance between the two m1 assemblages, both in morphology and in the means and distributions of measurements and ratios (Fig. 12). Paulson (1961) notes that some 20% of the *M. paroperarius* m1's from the Cudahy local fauna are five triangled. The 59 measurable m1's in UMMP: V40299 from Sunbrite contain 8–9% of five-triangled variants. The median test (Dixon and Massey, 1969) yielded $\chi^2 = 0.3164$ (1 df.) in the comparison of the B/W distributions of *M. paroperarius* from Sunbrite and Cumberland, not indicating a significant difference. It is possible that Paulson included some five-triangled variants of *M. meadensis* in his counts. This is concluded from the presence of seven five-triangled *M. meadensis* variants in vial V40299 (evidently picked for *M. paroperarius*). *M. meadensis* is distinguished from *M. paroperarius* by the better developed anterior loop of the former. On this criterion the *M. paroperarius* m1's of Paulson (1961: Figs. F and G) belong to *M. meadensis*. Neither Hibbard (1944)

nor Paulson (1961) have described five-triangled variants of *M. mead-ensis*.

Microtus paroperarius is additionally known from the Vera local fauna (Hibbard and Dalquest, 1966) and Conard Fissure (Graham, 1972). In both these localities, it is a rare species.

Guthrie and Matthews (1971) described *Microtus deceitensis* from the Cape Deceit fauna in Alaska and point out that the m1 of their species is simpler than that in *M. paroperarius*, whereas its m3 is unusual for *Microtus* because of the deep first buccal reentrant. The lengths of m1 of *M. deceitensis* range from 3.1 to 3.95 mm (Guthrie and Matthews, 1971: fig. 8), which are very high values for any *Microtus* and are much higher than those for *M. paroperarius*. The M3 associated with *M. paroperarius* are the normal three-triangled variants found in many extant species, whereas those of *M. deceitensis* are more simple (Guthrie and Matthews, 1971: 489).

Comparison to Related European Species

Hibbard (1944) noted the morphological resemblances between *M. paroperarius* and *M. ratticepoides* Hinton, 1923 from the Upper Fresh-water Beds near West Runton in England. He also noted the unclear separation of *M. ratticepoides*, *M. nivalinus* Hinton, 1923, *M. niva-loides* F. Major, 1902, and *M. arvalinus* Hinton, 1923. The latter three species also have West Runton as their type locality, and at least the first three should be included in a single species—*M. nivaloides* (Van der Meulen, 1973). Pending a revision of *Microtus* from West Runton the author distinguished *Microtus* sp. C from Villány-8 and *Microtus* sp. D from Villány-6 in Hungary (Van der Meulen, 1973). The latter contains more five-triangled variants than the former, which predom-inantly consists of four-triangled *M. ratticepoides* variants. *M. paro-perarius* resembles *Microtus* sp. C both in size and morphology, and differs only in a higher mean A/L value. The median tests on the differences between the A/L distributions of *M. paroperarius* from Cumberland Cave and Cudahy and *Microtus* sp. C from Villány-8/10 yielded $\chi^2 = 16.499$ and $\chi^2 = 15.936$, respectively. These χ^2 values largely exceed χ^2 99% = 6.635 (1 df.).

Both *Microtus* sp. C and *M. paroperarius* closely resemble the living species *M. oeconomus* (=*M. ratticeps*) in Eurasia and *M. operarius* in North America. The specific separation (if correct) of the living (Ognev, 1964) and fossil species is not reflected in their dental mor-phology, except that only in *M. paroperarius* M3, T2, and T3 are often communicating.

Microtus deceitensis is unique in size and in its combination of den-tal characters of m1, m2, and M3. It apparently constitutes an early side branch of *Microtus* evolution, and cannot, in my opinion, be re-

Table 4.—*Measurement and ratio data for ml's of* Microtus meadensis *from the Sunbrite (Cudahy) Ash Mine, Kansas.*

Parameter	N	Mean ± SE	SD	Range
L	99	2.883 ± 0.016	0.156	2.45–3.40
A/L	99	53.4 ± 0.17	1.67	48–58
B/W	117	<5.5		0–5
C/W	117	18.7 ± 0.45	4.88	3–30

garded to be the ancestor to *M. paroperarius* or *Microtus* sp. C, as thought by Guthrie and Matthews (1971). The more probable ancestor to these species is the predominantly three-triangled *Microtus burgondiae* Chaline (1972) = *Microtus* sp. B, Van der Meulen (1973), which has a more complicated AC2 than the four-triangled *M. deceitensis*.

With this interpretation of *M. deceitensis*, there is no other North American vole species left that can be considered to be intermediate between *Microtus* sp. from Wathena and Kentuck and *M. paroperarius*. It is assumed that *M. paroperarius* is another Eurasian immigrant, directly descending from *Microtus* sp. C (see below).

Comparison of Microtus meadensis *Hibbard and* Microtus arvalidens *Kretzoi*

Associated with *Microtus paroperarius* and *M. llanensis* from the Cudahy fauna is *M. meadensis*. Hibbard (1944) in his original description noted the resemblance of *M. meadensis* m1's with those of *M. arvalidens* (=*"Pitymys"* *arvaloides* Hinton), which is known from many Middle Pleistocene localities in Europe and is often associated with *Microtus* sp. C. Although Hibbard placed *M. meadensis* in the subgenus *"Pitymys,"* he notes after comparisons with *P. nemoralis*: "The patterns of m1 and m2 of *Pitymys meadensis*, *P. arvaloides* and *P. gregaloides* seem more closely related to the living genus *Neodon* of southeastern central Asia than to our living forms of *Pitymys*" (Hibbard, 1944: 732). In the present paper, it is confirmed that *Microtus meadensis* and *M. arvalidens* are not related to the living American *Pitymys* (see section on the taxonomy of *Pitymys*). *Microtus meadensis* is largely different from the probably slightly older *Pitymys cumberlandensis*, new species, from Cumberland Cave and the contemporaneous or slightly younger *P. cumberlandensis* from Conard Fissure (see below).

One hundred thirty-seven measurable m1's (UMMP V43938) of *M. meadensis* from its type locality, the Sunbrite Cudahy Ash Mine (Univ. of Kansas Locality 17), have been studied (Table 4) and compared to *M. arvalidens* from Nagyharsányhegy-4 and Villány-6 in
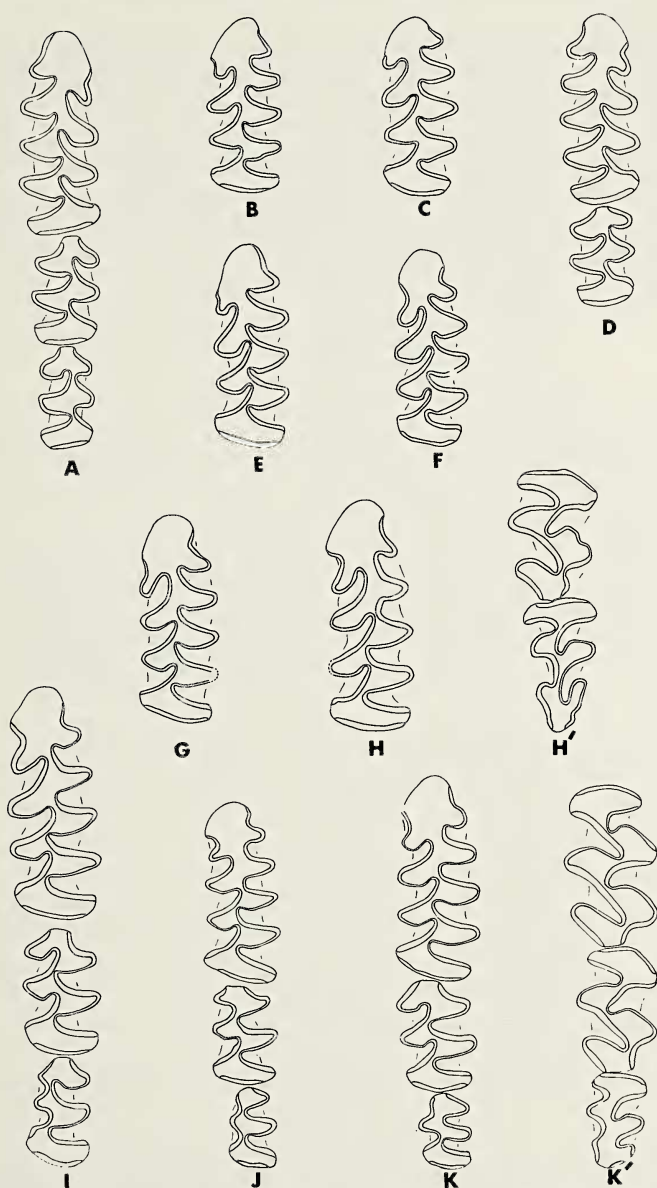
Fig. 13.—*Pitymys cumberlandensis*, new species, from Cumberland Cave, Maryland—A) right m1-m3, CM 20338, holotype; B) left m1 from unnumbered sample; C, E–G) left m1 from sample CM 20412; D) right m1-m2, CM 20378. *Pitymys pinetorum scalopsoides* from Lawrence Co., Pennsylvania—H, H′) left m1 and right M2-M3, CM 26727. *Pitymys pinetorum nemoralis* from Adair Co., Oklahoma—I) left m1-m3, USNM 87253, topotype. *Pitymys pinetorum pinetorum*—J) left m1-m3, USNM 276510. *Pitymys pinetorum parvulus* from Ocala, Florida—K, K′) left m1-m3 and right M1-M3, USNM 210487.

southern Hungary. The mean of L of m1 of *M. meadensis* is larger than that of the European assemblages. The mean of A/L (relative length of the anteroconid complex) of the former is somewhat larger than that found for the *M. arvalidens* from Villány-6, its mean of C/W (communication between T4 and T5) value is somewhat smaller. The differences with *M. arvalidens* from Nagyharsányhegy-4, which is somewhat more primitive than *M. arvalidens* from Villány-6, are greater. The figures confirm Hibbard's observation of the close resemblances between *M. meadensis* and *M. arvalidens*.

Pitymys cumberlandensis, new species
Figs. 11J–M, 13A–G

Holotype.—Damaged, right mandible m1–m3, Fig. 13A; CM 20338.
Figured paratypes.—Fig. 11K; Fig. 13C, E–G.
Horizon and type locality.—Irvingtonian cave filling of Cumberland Cave, near Cumberland, Maryland.

Derivatio nominis.—Named after the type locality.
Referred specimens.—From Cumberland Cave collection at Carnegie Museum—Fragmentary jaws with one or more molars: CM 20334, CM 20335, CM 20344, CM 20346, CM 20361, CM 20363, CM 20378, CM 20382, CM 20393, CM 24245, CM 24263–24264; isolated m1's: CM 20409–20410, CM 20416 (9 m1's), no number (14 m1's); isolated M3's: CM 20416 (21 M3's). From Cumberland Cave collection at USNM—USNM 12602. From Conard Fissure collection at the State University of Iowa—SUI 35727-B, no. 1; SUI 35736/L.

Diagnosis.—A *Pitymys* species with molars that show very little differentation of the enamel thickness and with m1 in which BRA4 and LRA5 are shallow and rarely contain crown cementum, and with unreduced m3 and M3.

Differential diagnosis.—*Pitymys pinetorum* and *P. parvulus* have a more reduced m3 and M3 than *P. cumberlandensis*. *P. pinetorum scalopsoides* m1's have better developed reentrant angles on the anterior cap than *P. cumberlandensis*. The molars of *P. nemoralis* have more differentiated enamel, whereas the communication between AC2 and T4–T5 is narrower than in *P. cumberlandensis*.

Measurements.—See Table 1, 5. The holotype: m1–m3 = 5.31; a = 1.24, L = 2.60, W = 0.97, w' = 0.87, b = 0.14, c = 0.12, A/L = 48, W'/W = 90, B/W = 14, C/W = 12.

Description

m1.—The description of m1 is based on 90 specimens. The occlusal surface shows an enamel pattern of a PL, three triangles, and a fairly complicated ACC consisting of two triangles (T4 and T5) and a broad AC2, which is usually bearing well-developed BSA4 and LSA5 and incipient BRA4 and LRA5. Narrow communications are regularly present between T1, T2, and T3. The communication between T1 and T2 may be broad. The enamel is thick. Its thickness is normally reduced at the anterior parts of the reentrants. The reentrant angles are narrow and deep. The buccal ones are almost as deep as the lingual ones. The tips of the salient angles are not pointed in most specimens. Two out

of the 67 specimens of CM 20416, 20412, and an unnumbered sample have crown cementum in LRA4, one in BRA4, and two in both reentrants.

m2.—All 11 m2's associated with *P. cumberlandensis* m1's consist of three dentine fields.

m3.—Also the occlusal surface of this molar consists of three dentine fields. The buccal salient and reentrant angles are little reduced.

M2.—Four M2 from sample CM 20416 are assigned to *P. cumberlandensis* on the basis of thick enamel. Three of them are remarkable for having a narrow fold at the anterobuccal side of T3. The shallow posterior folds have no crown cementum.

M3.—Twenty-one M3's from CM 20416 are assigned to *P. cumberlandensis*. Behind the oblique AL follow two broadly confluent, opposing triangles and a short posterior loop (PL), which is provided with two salient angles and usually, two very shallow folds. The PL may bear an additional dentine tract (Fig. 6b).

Remarks on Pitymys *McMurthrie 1831*

The type species of *Pitymys* is *P. pinetorum* (Le Conte), the North American pine vole. Its dentition shows thick, little-differentiated enamel, more or less rounded salient angles, and rather narrow reentrants. The buccal reentrants of the three-triangled m1 have aptly been described as "anteriorly oriented half crescents" by Paulson (1961: 148), and are unlike those in *Microtus* m1's in which the posterior part of the buccal reentrants are bent medially. *Microtus* dentitions differ further in having fairly thin well-differentiated enamel, pointed salient angles, and wide reentrants.

The eastern *Pitymys pinetorum* (with subspecies *pinetorum*, *scal-opsoides*, and *auricularis*), *P. parvulus* from Florida and the western *P. nemoralis* form a closely related group of species (Fig. 13H–K). The latter two are usually considered as subspecies of *P. pinetorum*. There are, however, consistent dental differences, which a paleontologist would not hesitate to translate in specific separation. In *P. pi-netorum* m3 and M3 may be a little reduced in size relative to the other elements. In *P. parvulus*, however, the m3 and M3 are conspicuously reduced in size, and the M3 often shows a single dentine field at the occlusal surface, wheras there are three or four in *P. pinetorum* due to the greater depth of the reentrants. *P. nemoralis* is larger than the two other species, the enamel is better differentiated and the connection between anterior cap and T4–T5 in m1 is narrower. The M3 and m3 of *P. nemoralis* are not reduced. The shape of the salient and reentrant angles may be somewhat *Microtus*-like, but the unreduced parts of the enamel are thick as in *P. pinetorum*.

P. cumberlandensis, thus far known from Maryland and Arkansas, is regarded as the ancestor of the three *Pitymys* species mentioned above. Its dentition fits the characteristics of *Pitymys*. It is more primitive than the living representatives in the virtually undifferentiated enamel and in the less elaborate anterior cap. The latter observation is illustrated by the fact that two out of 67 m1's of *P. cumberlandensis*

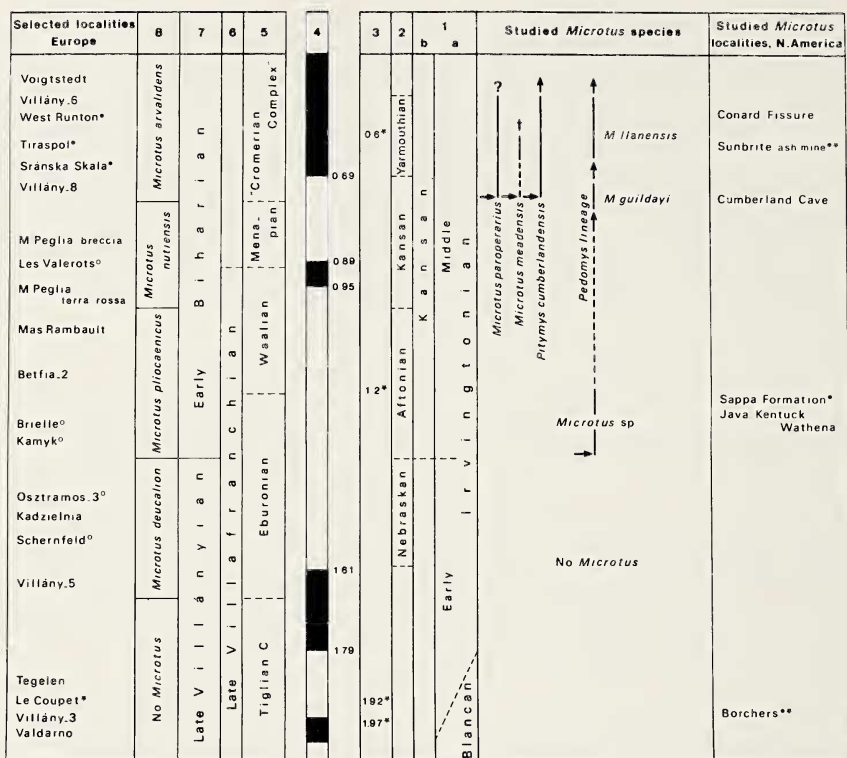| Selected localities Europe	8	7	6	5	4	3	2	1 b	1 a	Studied Microtus species	Studied Microtus localities, N.America
Voigtstedt / Villány.6 / West Runton* / Tiraspol* / Sránska Skala* / Villány.8	Microtus arvaldens	Biharian	"Cromerian Complex"	Mena-pian	0.69	0.6*	Yarmouthian			? M llanensis	Conard Fissure / Sunbrite ash mine**
M Peglia breccia / Les Valerots○ / M Peglia terra rossa	Microtus nutiensis			Waalian	0.89 / 0.95		Kansan	Kansan	Middle	M guildayi	Cumberland Cave
Mas Rambault / Betfia.2 / Brielle○ / Kamyk○	Microtus pliocaenicus	Early				1.2*	Aftonian		Irvingtonian	Microtus paroperarius / Microtus meadensis / Pitymys cumberlandensis / Pedomys lineage / Microtus sp	Sappa Formation* / Java Kentuck / Wathena
Osztramos.3○ / Kadzielnia / Schernfeld○ / Villány.5	Microtus deucalion			Eburonian	1.61		Nebraskan			No Microtus	
Tegelen / Le Coupet* / Villány.3 / Valdarno	No Microtus	Late Villányian	Late	Tiglian C	1.79	1.92* / 1.97*	Early		Blancan		Borchers**

Fig. 14.—Correlation chart between Irvingtonian and Biharian *Microtus* faunas with the aid of absolute and magnetic datings. Absolutely dated localities and paleomagnetically studied localities are indicated with an asterix and a solid circle, respectively. The absolute dates are given in column 3.

The succession of the studied *Microtus* localities is given in the far right column. The absolutely dated Sappa Formation (with *Microtus*) and Borchers locality (without *Microtus*) are added. The succession of the former localities is based on the steps in the *Pedomys* lineage. Correlation with the Irvingtonian land mammal stage (column 1a) is discussed in the text. Different opinions on the criteria to recognize the Irvingtonian and Blancan (for example, Hibbard, 1972; Zakrzewski, 1975) are expressed by the obliquely drawn boundary between these two stages. Column 1b shows the use of the Kansan Glacial Stage by vertebrate paleontologists (for example, Zakrzewski, 1975). For comparison Berggren and Van Couvering's (1974: Fig. 14) calibration of the North American climatic stages (column 2) with the Standard palaeomagnetic time scale by Cox (1969) (column 4) is given.

The succession of the selected European localities is based on voles and follows from the author's (1975) biozonation (column 8) of the Late Villányian and Early Biharian of the Hungarian Pleistocene subdivision by Kretzoi (1941). An open circle accompanying some localities indicates the presence of lemmings in today's temperate zone of Europe marking cool climate. The evidence for the correlation between the Hungarian and Dutch subdivision (column 5) is discussed in the text. The correlation of the sequence of the latter to the paleomagnetic scale is from Zagwijn (1975: Fig. 8) which in its turn

Table 5.—*Measurement and ratio data for ml's of* Pitymys cumberlandensis, *new species, from Cumberland Cave.*

Parameter	N	Mean ± SE	SD	Range
L	45	2.535 ± 0.023	0.151	2.28–2.87
A/L	45	48.2 ± 0.36	2.38	44–53
W'/W	42	92.6 ± 0.63	4.06	84–102
B/W	42	16.2 ± 0.82	5.30	6–27
C/W	42	15.1 ± 0.79	5.10	6–32

show cement in the fourth buccal reentrant as opposed to 56 out of 112 in *P. pinetorum* from the Recent sink hole to New Paris 2 (Guilday et al., 1964). This indicates the better development of BRA4 in the living representative, because cement is present only if the reentrant has reached a certain depth.

P. cumberlandensis cannot be derived from a known *Microtus* species, because in its thick enamel, rounded salient angles, and narrow reentrants it is more primitive than even the oldest *Microtus* (*Allophaiomys*).

It is concluded that the *Pitymys* species discussed here form a separate genus of unknown origin with distinct dental characteristics of unknown origin. The genus does not include *Microtus meadensis* from the Cudahy fauna, which have *Microtus* type molars. *M. oaxacensis* has not been seen. *Microtus quasiater* molars resemble those of *M. meadensis*. The separated anterior cap in m1 is somewhat less elaborated in the former and a number of variants closely resemble the fossil *M. gregaloides* from Europe. It has been proposed that *M. quasiater* is a disjunct western representative of a cline connected to *P. pinetorum* through *P. nemoralis*. This cannot be disproved on dentitions alone, but seems unlikely. Although intermediate in the degree of separation of the anterior cap, *P. nemoralis* has thick enamel, and the general shape of salient and reentrant angles is quite unlike *P. quasiater*, in which the enamel is thin, the salient angles pointed, and the reentrants wide as in *Microtus*.

This study does not include living "*Pitymys*" from Eurasia. Judging from Chaline's (1972) excellent figures at least some of them (for example *P. duodecimcostatus* and *P. lusitanicus*) may belong to the American genus. Supposedly true *Pitymys* forms appear in France in

←

is mainly based on Van Montfrans (1971). Azzarolli's (1970) correlation of the Late Villafranchian (column 6) with the Dutch sequence is added for reasons of comparison (see text).

Late Middle Pleistocene localities, such as Nestier and Lazaret. The molars determined as *Pitymys subterraneus* from Saint-Estève-Janson (Chaline, 1972) and the Biharian (Middle Pleistocene) *Microtus arvalidens* and *M. gregaloides* do not belong to *Pitymys* in which they have been traditionally placed. Their general dental characteristics are those typical of *Microtus* (*Allophaiomys*) (Chaline, 1972; van der Meulen, 1973).

AGE OF THE CUMBERLAND CAVE FAUNA

The biostratigraphic position of the Cumberland Cave deposits will be based on the arvicolids alone, the evolutionary stages of *Microtus* and *Ondatra* in particular. Presently the following list of the lemming and vole assemblage can be given (after Gidley and Gazin, 1938; Guilday, 1971; Zakrzewski, 1975; and the author's observations): *Synaptomys cooperi* Baird; *S.* (*Mictomys*) sp.; *Ondatra annectens* (Brown); *Atopomys salvelinus* Zakrzewski; *Phenacomys* sp.; *Clethrionomys* cf. *gapperi* (Vigors); *Pitymys cumberlandensis*, new species; *Microtus guildayi*, new species; *M. paroperarius* Hibbard. Guilday (1971) assigned a pre-Wisconsin, supposedly Illinoian age to Cumberland Cave. Recently Zakrzewski (1975: 261) remarked: "If the Cumberland Cave local fauna had been located on the Great Plains, the association of *Ondatra annectens*, *Neofiber*, and *Atopomys*, and the lack of *Microtus pennsylvanicus*, would suggest a pre-Illinoian age." *Neofiber* is not present in Cumberland Cave, as was stated by Guilday (1971).

The study of *Microtus* confirms Zakrzewski's suggestion (Fig. 14). *M. guildayi* is closely related to *M. llanensis* from the Cudahy, Vera and Conard Fissure local faunas from the Great Plains and Ozarks. In all three faunas *Ondatra annectens* and *Microtus paroperarius* are present, whereas *Pitymys cumberlandensis* occurs in Conard Fissure. These distributions point to a close relationship in age of the mentioned localities. Cumberland Cave is thought to be the oldest because *M. guildayi* is somewhat more primitive than *M. llanensis* The compared localities from the central U.S. have all been assigned to the Kansan Glacial Stage, and to the Irvingtonian Mammal State (for example, Hibbard, 1970; Hibbard and Dalquest, 1966; Graham, 1972) and to the middle part of the Irvingtonian by Zakrzewski (1975).

Other localities in the Midwest assigned to the Kansan and Irvingtonian are Kentuck (Hibbard, 1952; Semken, 1966; Zakrzewski, 1975), Wathena (Einsohn, 1971; Zakrzewski, 1975), type Sappa Formation (Schultz and Martin, 1970), and Java (Martin, 1973). The *Microtus* from these localities are more primitive than *M. guildayi*, and indicate an older age than Cumberland Cave and Cudahy. The latter is generally considered to be Late Kansan. Martin (1973) already considered Java to be older than Cudahy. Dreeszen (1970) consideres the Nickerson

Till that overlies the fossiliferous beds at Wathena as Early Kansan. The Type S Pearlette Ash (Coleridge ash) in the type Sappa Formation dates 1.2 m.y., whereas the Type O Pearlette Ash overlying the Cudahy fauna is dated as 0.6 m.y. These dates are in accordance with the biostratigraphical sequence suggested by the *Pedomys* lineage, but are not consistent with correlations in the literature. The fauna from the Sappa Formation is thought to be a Cudahy equivalent by Schultz and Martin (1970) and is placed in the Late Kansan by these authors and Dreeszen (1970).

Study of *Microtus* cf. *llanensis* from the Sappa Formation is, therefore, needed. If it resembles the Wathena *Microtus* (Einsohn, 1971: 65, Pl. 8, Figs. 1–3, 5–8), and is more primitive than the Cudahy *M. llanensis*, it will be difficult to maintain age differences between Wathena and Sappa and age equivalency of Sappa and Cudahy.

There is a further discrepancy between the succession based on *Microtus* and that on *Ondatra* (Semken, 1966; Nelson and Semken, 1970), which shows two trends utilizing length and width of the first lower molar and the height of the first labial dentine tract.

In my opinion the discrepancy arises merely from the independent use of the two parameters in *Ondatra*. Dentine tracts are those vertical areas along salient angles by which high crowned arvicolid molars are attached to the alveolar walls (Mahn, 1890). Their development and increase in height (independent of size increase of the molars) permit the molars to become high crowned and, eventually, unrooted in the course of evolution, as they take over the function of roots. So, although the distributions of length and width of the m1's made by Semken give information only on size, the distribution of dentine tracts reflects a combination of size and hypsodonty. It would, therefore, be worthwhile to compute the length/dentine tract height ratios of *Ondatra* and *Pliopotamys* in order to test the increase of hypsodonty independent from size variations.

All *Ondatra* m1's from Wathena and most of them from Kentuck are larger than the Cudahy m1's and both Semken (1966) and Einsohn (1971) conclude that Cudahy is older than the first two mentioned localities. However, the dentine tracts are of the same height in all three assemblages. This indicates that the Wathena and Kentuck specimens are more primitive, because the relative heights of their dentine tracts are lower than in the Cudahy specimens.

The size of the m1's in living *Ondatra* is variable and shows a definite correlation with latitude; northern populations are larger than more southern ones (Nelson and Semken, 1970). The presence of two size groups of *Ondatra* in Kentuck (and a few other localities) may be explained by assuming glacial-interglacial shifts of biotopes during deposition. In conclusion, the *Ondatra* chronocline does not disprove

the succession resulting from the *Pedomys* lineage, and in fact, it can be easily matched.

The two measurable *Ondatra annectens* m1's from Cumberland Cave (5.1 and 5.3 mm) are a trifle smaller than the Cudahy m1's (5.4–6.0 mm). Dentine tracts could not be measured due to the advanced stage of wear of the Cumberland specimens.

The suggested Middle Irvingtonian age of Cumberland Cave makes the presence of *Synaptomys cooperi*, *Clethrionomys* cf. *gapperi*, *Pitymys*, and *Microtus paroperarius* the oldest North American occurrences of these taxa. *Phenacomys* is present in the Java local fauna (Martin 1973).

Synaptomys (*Mictomys*) sp. from Cumberland Cave differs from the living *S. borealis* in the absence of crown cementum in the posterior buccal reentrant of m3 and in the shapes of the two middle lingual salient angles of m1 (LSA2 and LSA3). In *S. borealis* LSA3 is much narrower than LSA2, whereas the posterior wall of LSA2 (also in m2) is concave. In the Cumberland Cave m1 LSA2 and LSA3 are subequal (LSA3 may be slightly narrower) and the posterior side of LSA2 is convex (also in m2). In these characters *S.* (*Mictomys*) sp. from Cumberland resembles *S.* (*Mictomys*) *kansasensis* from Kentuck, Wathena, and Java and *S.* (*Mictomys*) *meltoni* from Cudahy. However, in the latter two species the enamel thickness differentiation is extreme, whereas it is hardly noticeable in Cumberland molars. The living and fossil species are all closely related.

Atopomys salvelinus is slightly more advanced than *A. texensis* from Fyllan Cave, which is accompanied by a *Microtus* species closely resembling *M. guildayi* (Zakrzewski, 1975 and the author's observations). Zakrzewski (1975) thinks that *A. texensis* is not directly ancestral to *A. salvelinus* because the latter has a more simple anterior loop than the former. He is, however, mistaken when he states that a trend towards simpler loops is not yet known among arvicolids. In several lineages of *Mimomys*, for instance, crenulations are lost and islets and ridges are more and more restricted to younger ontogenetic stages (for example, Forsyth Major, 1902; Kretzoi, 1969). This results in more simple patterns in later species. There seems to be no impediment to deriving *A. salvelinus* from *A. texensis* and, for that matter, *Atopomys* from *Nebraskomys*.

Thus far *A. salvelinus* from Cumberland Cave and Trout Cave are the latest known occurrences of the genus.

Intercontinental Migrations of *Microtus* during the Middle Irvingtonian

The comparisons of the Middle Irvingtonian/Kansan *Microtus* with Early Biharian relatives from Europe resulted in the recognition of

three pairs of closely resembling species. These are *Microtus mead-ensis-M. arvalidens*, *M. paroperarius-Microtus* sp. C (from, for instance, Villány-8; van der Meulen, 1975), and *Microtus* sp. (from Wathena and Kentuck)-*M. pliocaenicus*.

The similar dental morphologies in these species on both sides of the Bering Strait are definite evidence for the occurrences of migrations. On the basis of the compared species a correlation of Middle Irvingtonian and Early Biharian seems to be suggested. Dental morphology alone, however, does not permit such a conclusion, because of possible and demonstrated differences in rates of evolution in different parts of the Holarctic. For instance, dentitions such as found in *Microtus* (*Allophaiomys*) sp. and *M.* (*Allophaiomys*) *pliocaenicus* are restricted to the Irvingtonian in North America and to the earliest part of the Biharian in Europe, but are still present in some living species of *Microtus* (*Phaiomys*) in Asia. To limit the timespan during which the migrations took place one has to look for well-established correlations between the two areas.

In North America there are two absolute dates directly related to *Microtus* bearing sediments (Zakrzewski, 1975). The Coleridge Ash, dated 1.2 m.y. overlies *Microtus* sp. bearing beds in the type section of the Sappa Formation. *M. paroperarius* and *M. meadensis* of the Cudahy local fauna occur in normally magnetized sediments directly underlying the Pearlette Type "O" ash dated 0.6 m.y. This evidence indicates an early Brunhes age of the magnetic time scale (Lindsay et al., 1975). In addition there is the date of ± 2 m.y. for the Early Irvingtonian fauna (without *Microtus*) of Borchers (Hibbard and Dalquest, 1973).

There are no absolute dates for *Microtus* faunas in Europe. Paleomagnetic studies of the Tiraspol section (Nikiforova et al., 1970) in Russia, Stránska Skála in Czechoslovakia (Kukla, 1971), and the Upper Freshwater Bed of the Cromerian type section in East Anglia (Van Montfrans, 1971), indicate that the 0.7 m.y. Matuyama-Brunhes boundary falls in the third, *Microtus arvalidens* Zone (Van der Meulen, 1973 to replace the Nagyharsányhegy and Templomhegy phases of Kretzoi, 1965) of the Biharian. The pre-*Microtus* fauna from Saint Gorges d'Aurac, France, below the Coupet basalt, has been dated as 1.9 m.y. (Chaline and Michaux, 1969). It has been considered that *Microtus* immigrated into Europe at about the beginning of Eburonian, which falls in the Gilsa event, ± 1.6 m.y. (Van Montfrans, 1971; Van der Meulen and Zagwijn, 1974).

The absolute dates and paleomagnetic evidence show that the compared *Microtus* lived during the same time interval. This conclusion greatly increases the significance of the observed morphological similarities of the species in question.

It seems safe to assume that Eurasia was the evolutionary center. Although little is known from Asia, the studies of Chaline (1972) and Van der Meulen (1975) lead to the recognition of gradual changes during the Biharian of Europe starting with the Late Villányian *M. deucalion*, which is the most primitive known representative of the genus. The author (Van der Meulen, 1973) has estimated a very rapid development of *Microtus* during the Villányian-Biharian in Europe. Since that paper was submitted (1972), it became clear that *M. deucalion* is a valid species (Van der Meulen, 1974) and that the Matuyama-Brunhes boundary should be correlated to the *M. arvalidens* Zone of the Biharian (see above). Therefore, it can now be estimated that the development from *M. deucalion* to *M. arvalidens*, *M. gregaloides* and *Microtus* sp. C, each of these three lineages consisting of four recognizable successive steps, took place in ±1 m.y. It is assumed that the *Microtus* evolution in Asia of which there are only few data available to the author, did not develop more rapidly than in Europe.

Accepting Eurasia as the evolutionary center of *Microtus* during the considered time interval, and the high evolutionary rate of *Microtus* development in Europe as maximal, the dating of *Microtus* species immigrations into North America may be given as maximal ages in terms of European stratigraphy.

Bearing the above data and assumptions in mind, the following conclusions are drawn.

1) The immigration of the Wathena and Kentuck *Microtus* took place during the earliest part (*M. pliocaenicus* Zone, Van der Meulen, 1973 = Betfia phase, Kretzoi, 1965) of the Biharian; probably during the end of Eburonian. In recent literature the immigration of *Microtus* in Europe has been taken as the event marking the beginning of the Biharian (Fejfar, 1976). This is not correct since the earliest *Microtus* (*Allophaiomys*) *deucalion*, is present in Villány-5, which Kretzoi (1956) included in the Villanyian on the predominance of *Mimomys*. The author follows Kretzoi and considers *M.* (*Allophaiomys*) *pliocaenicus* as marking the beginning of the Biharian. It follows that the immigration of *Microtus* sp. in North America does not predate the European Biharian, unless the *M. deucalion–M. pliocaenicus* evolution took place more rapidly in Asia than in Europe, which possibility has been rejected. Because *Microtus* sp. is in some respects slightly more primitive than *M. pliocaenicus* from its type locality, Betfia, which is placed in the middle part of the *M. pliocaenicus* Zone, its immigration is assumed to have taken place during the beginning of the range of *M. pliocaenicus* and, therefore, of the Biharian. The Villányian-Biharian boundary is straddled by the Eburonian, which in the Brielle boring yielded *M. pliocaenicus* (van der Meulen and Zagwijn, 1974). Hence, the conclusion is reached that *Microtus* sp. immigrated during the late

part of the Eburonian. The date of 1.2 m.y. for the *Microtus* sp. bearing fauna in the Sappa Formation is not inconsistent with an Early Bihar-ian/Late Eburonian immigration.

2) The immigration of *M. paroperarius* and *M. meadensis* took place during the early part of the *M. arvalidens* Zone (third and latest zone of the Early Biharian in Van der Meulen, 1973). *Microtus* sp. C and *M. arvalidens* appear simultaneously in the older localities (for in-stance, Villány-8) of the *Microtus arvalidens* Zone of the Biharian. They descend from *M. burgondiae* (=*M. (Allophaiomys)* sp. B in Van der Meulen, 1973) and *M. nutiensis* (=*M. (Allophaiomys)* sp. A in Van der Meulen, 1973) from the preceding Zone. It is premature to spec-ulate whether the absence of *M. meadensis* in Cumberland Cave in-dicates that *M. paroperarius* immigrated before *M. meadensis* did, considering the few data at hand. The absolute and paleomagnetic dates show that the immigration of the two American species followed very shortly their origin in Eurasia.

The two migrations into North America took place just prior to 1.2 m.y. and ±0.7 m.y. ago. The timespan embraced is represented by Lower Biharian sediments in Europe and Middle Irvingtonian sedi-ments in North America. Berggren and Van Couvering (1974) think that the Biharian follows the Villafranchian. In the author's opinion, the earliest part of the Biharian and Late Villafranchian are time equiv-alent. In European Russian localities (Kair and Nogaisk) and western Siberian sections (Kizikhan and Razdolian) Early Biharian arvicolids, *Microtus (Allophaiomys)* and *Prolagurus*, occur together with Late Villafranchian indicators such as *Elephas meridionalis* (see Kretzoi, 1965; Vangenheim and Zazhigin, 1972). The absence of such co-oc-currences in western European localities seems to be a result of the assemblages consisting of small or large mammals. In an as yet un-published fauna from southern Italy collected by Dr. M. Freudenthal, *Microtus pliocaenicus* and *Equus stenonis* are present. Other evidence contradicting Berggren and Van Couvering's estimate of 0.9 m.y. for the base of the Biharian is the evolution of *Microtus*, which would require more than the some 200,000 years permitted from their scheme.

The scarce finds of arvicolids in dated Dutch sections are all con-sistent with the biozonation given in Van der Meulen (1973). Presently these finds are *Microtus pliocaenicus* in the Eburonian (Van der Meu-len and Zagwijn, 1974), *M. burgondiae* in the Menapian (Van der Meu-len, 1973), and the unpublished find of *M. gregaloides* in Glacial A or Interglacial II sediments of the "Cromerian Complex," placed near the Brunhes-Matuyama boundary (Zagwijn et al., 1971). Thus, a cor-relation between Early Biharian and the Late Eburonian-"Cromeri-an" of the Dutch scale and Late Villafranchian-Cromerian of the tra-ditional European scale seems likely.

Lindsay et al. (1975) concluded that the Blancan-Irvingtonian bound-
ary falls in the early part of the Matuyama below the Olduvai event of
1.86–1.71 m.y. Faunistic changes by which they recognize the
boundary are the extinction of *Hypolagus*, *Borophagus*, and *Nannip-
pus* and the appearance of *Lepus*, *Dipodomys*, and *Ondatra*. Hibbard
and Dalquest (1973) place the Borchers fauna, dated 1.97 m.y., in the
Irvingtonian utilizing the same faunal criteria. Apparently the major
change in the arvicolid fauna was yet to come. The few vole species
in the Borchers fauna are the same as in typical Late Blanchan faunal
assemblages from Grand View and White Rock (Eshelmann, 1975).
The change in the arvicolids is characterized by the extinction of Blan-
can forms (for example, *Ophiomys*) and the appearance of *Microtus*,
which becomes the dominant vole. A similar change (rise to dominance
of *Microtus*, extinction of many *Mimomys* species) characterizes the
Villányian-Biharian boundary in Europe. It seems from our dating of
immigration of *Microtus* sp. and the few absolute dates of the Early
Irvingtonian and Late Villányian that the change took place at roughly
the same time in Europe and North America.

COMPARISON OF MIDDLE PLEISTOCENE *MICROTUS* EVOLUTION IN EUROPE AND NORTH AMERICA

The comparison is restricted to the Late Villanyian-Early Biharian
Microtus from Europe and their Middle Irvingtonian relatives in North
America. Data for the Asian development are insufficient for comment.

The evolution of European *Microtus* has recently been studied in
detail by Chaline (1972) and Van der Meulen (1973). In this section
only the pattern arrived at by the author is considered for reasons
explained in the next section.

Although Chaline and the author differ considerably on several as-
pects of *Microtus* dental evolution, they agree on the existence of the
main trends, which consists of complication of the anteroconid com-
plex of m1 in two different ways. Starting with a three-triangled m1
pattern with simple anterior loop characteristic of the subgenus *Allo-
phaiomys*, one lineage leads to the "*Pitymys*" pattern in which the
anteroconid complex is divided in two fields consisting of T4-T5 and
AC2. In the other, *Microtus*, lineage T4 and T5 and eventually AC2
are separated (Fig. 15). This evolution started with *Microtus deuca-
lion*, which immigrated to Europe during the Late Villányian (±1.6
m.y.). Toward the end of the Early Biharian, approximately 1 m.y.
later, at least four descendants were present—*M. arvalidens* and *M.
gregaloides* of the "*Pitymys*" lineage and *Microtus* sp. C and *Microtus*
sp. D (with different percentages of Hinton's 1926, *M. ratticepoides*,
M. nivaloides, *M. nivalinus*, and *M. arvalinus* morphotypes) of the
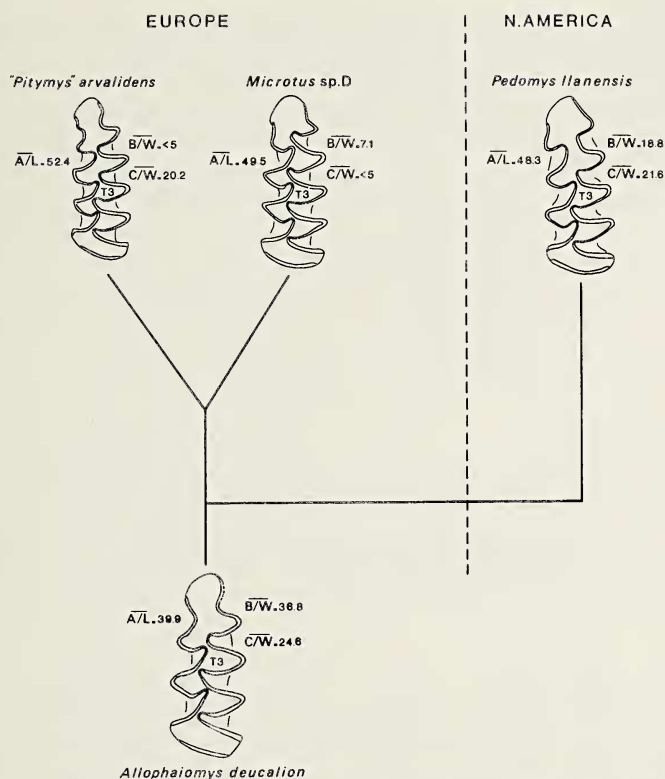*Microtus* lineage.

Fig. 15.—Simplified evolutionary scheme of early *Microtus* m1 in Europe and North America illustrating the different ways of complication of the anteroconid complex, which is the part in front of the third triangle, T3. The means of the ratios of the European species are from Van der Meulen (1973, 1974). *M.* ("*Pitymys*") *arvalidens* and *Microtus* sp. D are the most advanced Biharian species of the "*Pitymys*" and *Microtus* lineage, respectively. They are thought to be approximately contemporaneous with *M.* (*Pedomys*) *llanensis*. *M.* (*Allophaiomys*) *deucalion* is the oldest known *Microtus* species.

The relationships of the *Microtus* species to different biotopes has been discussed (Van der Meulen, 1973) from their differing frequencies in several small assemblages. The study lead to the recognition of three main factors involved in the rapid, branching evolution—a) the main trends are adaptive, b) the high rate of production, and c) climatic changes in the distribution area of the species forcing the populations to adapt or to migrate. Migration probably increased isolation of population groups each of which probably adapted to respective local environments.

No such rapid and diversified evolution seems to have taken place in North America during the Middle Irvingtonian, but it is realized that data are largely restricted to the Great Plains. As outlined before *Microtus* immigrated to North America somewhat more than 1.2 m.y. ago. This earliest species, *Microtus* sp. from Kentuck and Wathena, gave rise to *M. llanensis* (±0.6 m.y.) through *M. guildayi* in what is called the *Pedomys* lineage. The other two Middle Irvingtonian species, *M. paroperarius* and *M. meadensis*, are considered immigrants, because no intermediate species between these and *Microtus* sp. are known. It was also argued that *Pitymys cumberlandensis* (probably imigrating together with *Microtus paroperarius* and *M. meadensis*) and its living representatives form a separate group not to be included in *Microtus*. *M. deceitensis* from Alaska can be derived from any primitive *Microtus* species with a three-triangled m1 and a simple anterior loop, for example *M. pliocaenicus* or the Kentuck and Wathena *Microtus*. The partial separation of the middle triangles in m3, the asymmetrical anteroconid complex in which the buccal features are better developed than the lingual ones, and the combination of four-triangled m1 and two-triangled M3 do not allow *M. deceitensis* to be fitted into the known *Microtus* trends. The first two characters bar it from being ancestral to *M. paroperarius* Thus, *M. deceitensis* is considered to represent a separate *Microtus* lineage, possibly leading to *M. xanthognathus* with which is shares the m3 morphology (John Guilday, personal communication), and the asymmetrical anteroconid complex.

The *Pedomys* lineage is represented today by *Microtus* (*Pedomys*) *ochrogaster*. The overall change in m1 morphology is comparatively small in the *Pedomys* lineage because the m1 in the living *Microtus ochrogaster* are still three-triangled and more primitive than in any European species living 700,000 years ago. Another characteristic of the *Pedomys* lineage is the probable absence of side branches, whereas in Europe both *Microtus* and "*Pitymys*" lineages are each represented by two species in the late part of the Early Biharian. It seems that populations of *Pedomys* were not isolated long enough (if at all) for local adaptations to occur, in spite of the climatically forced migrations, which one may expect to have happened. The absence of major east-west barriers in the Great Plains, where *Pedomys* lives today, may explain the straight line development.

The European "*Pitymys*" and *Microtus* lineages and the *Pedomys* lineage seem to constitute a case history of parallel dental evolution. In each lineage, complication of the anteroconid complex takes place by enlarging existing and adding new salient and reentrant angles. This overall trend is reflected by the increase of the mean of A/L values standing for the relative length of the anteroconid complex (Fig. 15) in all three lineages. In the "*Pitymys*" and *Pedomys* lineage the mean
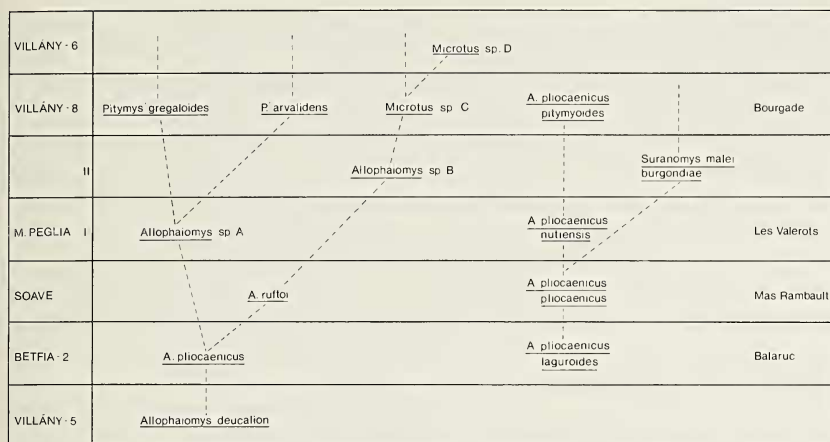
Fig. 16.—Comparison of the different determinations and resulting evolutionary rela-
tionships of early European *Microtus* species by Chaline (1972) at the right, and by Van
der Meulen (1973) at the left. The localities that yielded the m1's on which the two
schemes are based, are given. A taxon (or taxa) from the one scheme refers to the same
morphologies as the taxon (or taxa) from the other scheme placed at the same level.
Microtus (*Allophaiomys*) *ruffoi* is considered as a valid taxon by the author only.

of C/W (communication between T4 and T5) changes little, but in the
former the mean of B/W (communication between AC2 and T4-T5)
becomes much lower than in the latter. The *Microtus* lineage is pri-
marily characterized by the decrease of the mean of C/W; in *Microtus*
sp. D from Villány-6 the mean of B/W is also low, but not in *Microtus*
sp. C and *M. paroperarius* of the same lineage.

COMMENTS ON CHALINE'S MODEL OF EARLY BIHARIAN
MICROTUS EVOLUTION

The evolution of *Microtus* is a subject of potential interest not only
to the specialists of voles, but also to other students of evolution. The
author is convinced that it is possible to reconstruct, step by step, a
"family tree" of *Microtus* (and other vole genera as well) on a more
refined scale than is possible for many other animal groups.

It is, therefore, confusing that Chaline (1972, 1974) and the author
have developed quite different evolutionary patterns and interpreta-
tions of Early Biharian *Microtus* evolution in W. Europe. A preprint
of Chaline's thesis was kindly made available in 1972 to the author
before his thesis was in print, but too late to include an extensive
discussion on it. Since then Chaline (1974) has further expanded his
concepts on *Microtus* evolution to include all Holarctic species. Cha-
line and Michaux (1975) also have described a new example of vole

cladogenesis resulting from sympatric evolution following the same approach as in Chaline (1972). Only the Early Biharian part of the *Microtus* evolution will be discussed in this paper (Fig. 16).

On the basis of the material from the localities Balaruc, Mas Rambault, Les Valerots, and Bourgade, Chaline constructs his *Microtus* (*Allophaiomys*) *pliocaenicus* lineage as a series of successional subspecies—*laguroides*, *pliocaenicus*, *nutiensis*, and *pitymyoides*. In Les Valerots the subspecies *nutiensis* is accompanied by *Microtus* (*Suranomys*) *malei burgondiae*. These two forms are considered as two species *in statu nascendi*, representing an early phase of the branching off of the *Suranomys* lineage. Chaline hypothesizes that it is the result of sympatric speciation.

Fig. 16 shows the taxonomic nomenclature used by Chaline and the author. The following discussion attempts to show that the different evolutionary patterns follow from different interpretations of the variation in m1 morphology and from different methods in determination. Additionally there are different opinions on the validity of taxonomic names and on the type of classification to be followed—more vertical by Chaline and more horizontal by the author.

Microtus (*Suranomys*) Chaline 1972 is considered here to be the junior synonym of *M.* (*Chionomys*) Miller 1908, because it includes *M. nivalis*, which is the type species of the latter. It is possible that *Microtus* sp. C and D belong to *Chionomys* (van der Meulen, 1975: 100–101). Assigning *burgondiae* to the subgenus *Chionomys* or to *Allophaiomys* depends on the preference for the type of classification mentioned above. The same goes for the use of *M.* ("*Pitymys*") or *M.* (*Allophaiomys*) for the youngest forms of Chaline's *pliocaenicus* lineage (the author's "*Pitymys*" lineage).

Chaline's subspecies *laguroides* and *pliocaenicus* are based on *Allophaiomys laguroides* and *A. pliocaenicus* from Betfia, Roumania (Kormos, 1933). *A. laguroides* has been placed in the synonymy of *Microtus* (*Allophaiomys*) *pliocaenicus*, since Kormos' species could not be separated in topotype material (Van der Meulen, 1973). The Balaruc *laguroides*, I think, belongs to *M. pliocaenicus* from Betfia, despite the small size of the former. Judging from Chaline (1972: Fig. 20), *pliocaenicus* from Mas Rambault seems more advanced than the type material of *M. pliocaenicus*, and may be identical to *M. ruffoi* (Pasa, 1947), which Chaline synonymized with *M. pliocaenicus*. The present author regards this synonymy as doubtful.

In Les Valerots the same two species are present as in M. Peglia. They are both closely related to their common ancestor, *M. pliocaenicus* from Betfia. It has been shown that the author's *Microtus* sp. B is more similar to *M. pliocaenicus* than *Microtus* sp. A is (see mean A/L and mean B/W of the three species in Van der Meulen, 1973: Table 4).

It is proposed that the Les Valerots and M. Peglia taxa be named *Microtus* (*Allophaiomys*) *nutiensis* = *M.* (*Allophaiomys*) sp. A and *M.* (*Allophaiomys*) *burgondiae* = *M.* (*Allophaiomys*) sp. B, because it seems that vertical classification is carried too far if *nutiensis* is regarded as a subspecies of *pliocaenicus* while *burgondiae* is placed in another species and subgenus.

The separation and, hence, the characterization of the two taxa from Les Valerots as given by Chaline is considered unsatisfactory. The means and ranges of their m1 lengths are obtained from two artificial distributions which resulted from the arbitrarily cutting of the bimodal distribution for the total sample at one of the class boundaries. Furthermore, one of the histograms (Chaline, 1972: Fig. 27a), which is given to show the different morphology of the two size groups, is uninformative because the distribution is homogeneous and the various morphotypes are not indicated. In M. Peglia *M. nutiensis* and *M. burgondiae* occur separately in two different strata. The diagnoses based on these assemblages may, therefore, be more reliable than the original ones.

In the following quotation Chaline summarizes his arguments for the sympatric speciation of *M. nutiensis* and *M. burgondiae*. Discussing their m1 morphology he states (Chaline, 1974: 443–444): "L'existence de types morphologiques intermédiaires entre les deux groupes démontre que l'interfécondité devait être encore possible (au moins par la production de F1). Cette structure de population étant assez générale dans toute l'Europe pose la problème du déterminisme de cette cladogenèse qui ne semble pas s'expliquer par un isolement géographique. C'est pourquoi, j'ai proposé à titre d'hypothèse de travail, un processus éventuel de spéciation sympatrique où le facteur d'isolement intraspécifique pourrait correspondre à une modification de l'arrangement chromosomique favorisant les homozygotes. Les observations de R. Matthey (1964) sur les *Leggadas* montrent que ce schéma n'a rien d'invraisemblable."

The variations in dental morphology of many living *Microtus* show overlap of each other. This is easily explained by their close phylogenetic relationships, and does not necessarily imply cross breeding. Therefore, Chaline's conclusions, that *nutiensis* and *burgondiae* are two species *in statu nascendi* seems speculative. The discussed species are known with certainty from Les Valerots and M. Peglia only. Judging from the literature, they may occur in three or four other localities (Van der Meulen, 1973). So the above stated rather general co-occurrence in Europe is true for a small number of localities, but not for M. Peglia. Here they occur separately (in as much one can be certain, working with highly variable m1 morphologies) in the lower terra rossa and in the upper breccia. These beds produced quite different small mammal associations. Consequently, *M. nutiensis* and *M. burgondiae* were as-

sumed to have had different habitat preferences. Their succession in M. Peglia was explained by migrations caused by climatic change. In Les Valerots the taxa are found together in the same layers, but even then one must be careful in interpreting this fossil co-occurrence in terms of sympatry. This is shown, for instance, in the carefully sampled bed 12 of Villány 8 (Kretzoi, 1956; Van der Meulen, 1973). Conspicuous changes in the vertical distributions of species, indicating shifts of bio- topes, appeared to be present in this single layer (thickness ca. 50 cm).

In the opinion of the author these observations show that Chaline has not produced conclusive evidence opposing the conventional evolu- tionary reconstruction involving isolation (previous section), and sub- stantiating his attractive hypothesis of sympatric speciation.

Chaline's subspecies *pitymyoides* from Bourgade comprises hintonid/ gregalid, arvalid morphotype 3, and ratticepoid morphotype 2 first lower molars, corresponding to the present author's *Microtus gregaloides*, *M. arvalidens*, and *Microtus* sp. C, respectively. The supposed homogene- ity of *pitymyoides* has been based on the unimodal distribution of the m1 lengths (Chaline, 1972: Fig. 28), and on the presence of intermediates between most variants. Chaline notes that the ratticepoid molars are not connected by intermediates with the morphotype 3 molars. The present author found the same to be true in the assemblages from Nagyharsán- yhegy-4 and Villány-8, hence his separation of *Microtus* sp. C. Both in Villány-6 and Nagyharsányhegy-4 hintonid/gregalid (*M. gregaloides*) and arvalid molars (*M. arvalidens*) were separable on measurements of the characteristic anterior dentine field lying in front of the confluent pair of the fourth and fifth triangle typical of morphotype 3 (Van der Meulen, 1975: Fig. 31). The differences between the species recognized by the author are comparable to those between the living *M. arvalis*, *M. gregalis*, and *M. oeconomus*. Different habitat preferences of the fossil species are indicated in vole diagrams (Kretzoi, 1956; Fejfar, 1961; Van der Meulen, 1975). It follows that quantitative analysis of m1 length alone is considered insufficient to evidence the homogeneity of *pity- myoides*.

CONCLUSIONS

1. *Microtus* species, *M. guildayi*, new species, and *M. paroperarius*, and one *Pitymys* species, *P. cumberlandensis*, new species, are iden- tified in the Cumberland Cave fauna.
2. *Pitymys* is considered as a genus, that does not include "*Pitymys*" *arvalidens* and "*P.*" *gregaloides* from the Middle Pleistocene of Eu- rope. *Pitymys cumberlandensis*, the oldest known representative, does not descend from *Microtus* (*Allophaiomys*), which is the an- cestral stock of *Microtus*.
3. *Microtus* (*Pedomys*) comprises three North American species only—

the fossil *M. guildayi* and *M. llanensis*, and living *M. ochrogaster*. These species from a single evolutionary lineage descending from the unnamed *M.* (*Allophaiomys*) from Wathena, Kentuck, and Java, and probably the type section of the Sappa Formation. The latter *Microtus* is the oldest representative of the genus in North America.

4. The dental evolution in *Pedomys* is parallel to, but slower than, that in the European "*Pitymys*" and *Microtus* lineages.

5. The age of the Cumberland Cave fauna is Middle Irvingtonian *sensu* Zakrzewski (1975).

6. Two different migrations of *Microtus* from Eurasia into North America are distinguished. The earlier is the immigration of the Wathena and Kentuck *Microtus* at about the beginning of the Biharian, probably during the Eburonian glaciation, just prior to 1.2 million years ago. The immigration of *Microtus paroperarius*, *M. meadensis*, and *Pitymys cumberlandensis* took place just prior to 0.7 million years, at the beginning of the third, *Microtus arvalidens*, zone of the Biharian.

7. The Middle Irvingtonian is correlated to the Early Biharian.

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